

THE INTERACTION OF PHYSICAL AND BIOLOGICAL DETERMINANTS PRODUCING VEGETATION ZONATION IN TIDAL MARSHES OF THE SAN FRANCISCO BAY ESTUARY, CALIFORNIA, USA

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Abstract

The establishment and maintenance of tidal marsh ecosystems depends upon multiple interactions between tidal hydrology, local soil surface elevation, plant productivity, and regional salinity. The nature of these interactions, their relative influence on the character of the tidal marsh ecosystem, and their importance in determining the vegetation pattern on the landscape is not clearly understood. The research presented in this dissertation had four objectives: 1) to demonstrate the dependence of vegetation pattern on tidal channel hydrology; 2) to demonstrate that the strength of dependence of vegetation pattern on tidal channels changes with salinity; 3) to characterize the nature and quantity of the patterns of sedimentation within tidal marshes, and; 4) to provide conceptual models for understanding how physical and biological factors interact to produce and maintain tidal marshes, with an emphasis on aiding programs of tidal marsh restoration within the San Francisco Bay/Delta Estuary.

Rationale

Hydrologic investigations in tidal marshes have typically been concerned with siltation of larger-order channels and navigation (Schuepfer et al., 1988), while typical sedimentation studies have addressed issues of sea level rise and the ability of tidal marshes to “keep up” by trapping sediments over large expanses of the marsh plain rather than studying accretion processes occurring within specific tidal channel networks (Rejmánek et al., 1988; Nichols, 1989). Smaller-order channels (1st through 3rd orders) are younger and more dynamic in terms of sedimentation/erosion and in plan-form than larger-order channels (Collins, 1991). Importantly, these smaller-order channels have been shown to be critical to

the conservation of the marsh's tidal prism (Collins, 1991), and therefore to the persistence of the marsh itself (Pestrong, 1965; Collins et al., 1987). Previous studies of tidal marsh accretion/erosion and vegetation changes in response to tidal or salinity variations have typically ignored smaller-order channel network processes. Until recent findings suggested that smaller-order channel drainage network dynamics are important to tidal marsh evolution (Collins et al., 1987; Collins, 1995), or tidal marsh fauna (Garcia, 1995) there was little reason to study them. Until we improve our understanding of the interactions between the biological and physical processes within these smaller-order channel networks, efforts at enhancement, restoration, or creation of tidal marshes may be misdirected and ineffective (Josselyn and Buchholz, 1984). Understanding these relationships can allow resource managers to fine-tune salinities, water diversions, or plant community assemblages to maximize efforts at passive restoration of tidal marshes and establishment of appropriate drainage network vegetation.

Sedimentation and erosion of channels directly affects the volume of water a marsh can accommodate at bankfull stage (the tidal prism), and the longer-term accommodation of the tidal prism maintaining the marsh. Changes in a marsh's ability to accommodate a given tidal prism (disequilibrium between sedimentation/erosion rates, for example) can lead to changes in vegetation composition, hydrology, soil salinities, plant productivity, and sediment supply (Krone, 1993; Collins, 1995). These variations can ultimately result in a wholesale substitution of upland vegetation via classic succession stages, or degradation of the landscape (through flooding or salinity changes) back to tidal mudflat depending on the resulting hydrologic and edaphic conditions (Howard and Mendelssohn, 2000; Mitsch and Gosselink, 2000).

Understanding the influence of 1st through 3rd order channels requires knowledge of the sedimentation and vegetation productivity rates within particular channel drainage networks, and an understanding of the local effects of differing vegetation types on sedimentation adjacent to these smaller-order channels. Since tidal marsh plant species have different tolerances for soil salinity, flooding regime, and sediment accretion rates, and presumably exhibit differences in sediment trapping ability, any changes in any one or all of these influences can result in alteration of sedimentation, erosion, productivity, and plant composition within the marsh. Marshes at lower overall elevations (Mean Low Water and

lower) are presumed to be fundamentally different in character than marshes higher in the tidal range (Mean High Water and higher), and the geomorphological effects of their characteristic vegetation suites are likely to differ depending on local tidal marsh elevation.

Understanding how the processes of sedimentation and primary productivity are affected by changes in marsh vegetation (as caused by changing factors such as salinity, variable sediment supply, tidal prism, river discharge, etc.), can lead to predictions of how man-made manipulation of these factors might be expected to change the marsh landscape over meso-scale time periods (from weeks to years). As Collins and Foin (1992) have written in their Report to the *San Francisco Estuary Project*: “The functional relationships among biotic and abiotic processes that control the physical form and ecological functions of tidal marshland as a whole should be assessed. An understanding of the functional relationship between the growth of vascular vegetation and the evolution and maintenance of tidal marsh is especially important.”

Approach

Field surveys were used to identify underlying patterns within the tidal marsh landscape and to characterize the physical and biological influences important to forming and maintaining these patterns. Vegetation zonation across three different marshes spanning a range of tidal salinities within the Estuary was found to exhibit both similarity (channel-oriented distribution and abundance of species) and difference (changes in extent of vegetation zones, species substitution) between marshes, and was assumed to be due to the influence of either biological or physical forces. Experimental treatments were developed utilizing field and laboratory methods to selectively study the effects of hydrology, salinity, vegetation species identity, and geographic location on plant productivity, sediment deposition, and species abundance. Information from these surveys and treatments were then used to formulate a conceptual understanding of the relative influence of physical and biological processes on determining the nature of vegetation zonation in these marshes, and the subsequent role of this zonation in tidal marsh evolution and maintenance.

Findings

The strength of biological and physical determinants of tidal marsh vegetation zonation differs geographically. Regional salinity changes when moving from the Sacramento/San Joaquin River Delta to the Golden Gate in San Francisco Bay have pronounced effect on local soil salinity within Estuary tidal marshes. Local soil salinity is shown to be important to the identity and productivity of flora dominating these marshes. Conversely, tidal marsh plant species differ in their ability to tolerate soil salinity, and have variable productivity responses as a result. Local plant productivity and soil surface accretion through belowground biomass incorporation is thought to have important consequences for the continued existence of higher Estuary tidal marshes in the face of local sea level rise, salt water intrusion events, or other hydrologic manipulation. Biological interactions among native and invasive plant species may also show dependence on the strength of local physical gradients, with soil salinity an anticipated important mediator. Clearly, selection of anticipated target habitat identity and structure for programs of restoration within the Estuary depends upon variable species tolerance of soil salinities. Successful reestablishment of tidal marsh vegetation will depend upon utilization of species suites appropriate to local salinity and hydrologic conditions, and will be dictated by geographic position within tidal and salinity gradients found in the ecoregion.

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in Tidal Marshes of the San Francisco Bay Estuary, California, USA

By

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B.A. (Oberlin College) 1984

M.S. (University of California, Davis) 1993

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

Davis

Approved:

Committee in Charge

2001

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Acknowledgement

This dissertation is funded in part by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA66RG0477, project number R/CZ-154, through the California Sea Grant College System, and in part by the California State Resources Agency. The views expressed herein are those of the author(s) and do not necessarily reflect the views of NOAA or any of its sub-agencies. The U.S. Government is authorized to reproduce and distribute for governmental purposes. Grateful acknowledgment is also made to the Jastro-Shields Graduate Research Scholarship committee and the Graduate Group in Ecology Block Grant Fellowship committee at the University of California/Davis for their generous support.

As with most endeavors, this research would not have been possible without the kind and generous support of dozens of people too numerous to name. A few individuals deserve special mention, however, for guidance and patience displayed when supporting this work.

Thank you to my guidance/orals committees that ensured my preparation was appropriate to conducting ecological research: Dr. Caroline Bledsoe, Department of Land, Air, and Water Resources, Dr. Marcel Rejmánek, Evolution and Ecology, Dr. Peter Moyle, Department of Wildlife, Fish, and Conservation Biology, and Dr. Raul Piedrahita, Department of Biological and Agricultural Engineering. Special thanks to Peter and Raul for taking a real and personal interest in my pursuits and in my career, and for quiet but firm help during the more difficult periods of my graduate education.

Thanks to my dissertation committee for insistence on quality and completeness in the presentation of my research ideas and results: Dr. Theodore Foin, Department of Agronomy, Dr. Michael Johnson, John Muir Institute of the Environment, and Dr. Joshua Collins, San Francisco Estuary Institute. Particular thanks to Josh for getting me interested in all this stuff in the first place.

Special acknowledgement is made to Mr. Paul Bennick and Mr. Walter Pavlich for spiritual guidance during the unfolding of this work, and for helping me appreciate the less technical aspects of completing a course of graduate training. I could not have completed this work without your kind and generous understanding.

Finally, to Dr. Foin, who took an interest in my efforts in graduate school well before I began this program of research – thanks for keeping a place in the lab for me. I am grateful for the chance to bring this research to conclusion.

Steven D. Culberson

Davis, CA

September 2001

For Mary,
who is with me every step of the way;
and for Ben,
who makes each step adventurous.

The Relative Influence of Tidal Hydrology and Soil Salinity on Canopy Dominance in Marsh Vegetation of the San Francisco Bay Estuary

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Abstract

Previous research on Petaluma Marsh (San Francisco Bay, California, USA) revealed a clear pattern of vegetation zonation corresponding to a hydrologic zone of influence measured as distance from tidal channel. Similar research in two additional, less saline marshes within the Estuary showed reduced influence of the tidal channels. Soil surface elevations control local surface hydrology and are expected to be an important determinant of local vegetation pattern. When examined with respect to regional edaphic characteristics, however, elevation is a poor predictor of vegetation zonation. Local drainage network soil salinity strongly influences vegetation zonation within San Francisco Estuary marshes.

Introduction

Many tidal marsh studies have emphasized the dependence of tidal vegetation on the influence of the physical environment as a determinant of species zonation (Redfield, 1972; Mahall and Park, 1976a; Mahall and Park, 1976b; Mahall and Park, 1976c; Eleuterius and Eleuterius, 1979; Vince and Snow, 1984a; Vince and Snow, 1984b; Wilson and Keddy, 1986; Zedler and Beare, 1986; Earle and Kershaw, 1989; Wilson et al., 1996; Zedler et al., 1999; Howard and Mendelssohn, 2000). In particular, the influence of hydrology and prevailing soil characteristics have been shown to be correlated with broad patterns of vegetation zonation across different tidal marsh environments (Ustin et al., 1982; Percy et al., 1982; Vince and Snow 1984b; Howes et al., 1986; Pezeshki et al., 1987; Bertness 1991; Kenkel et al., 1991; Shipley et al., 1991; Bertness et al., 1992; Callaway and Sabraw, 1994; Sanchez et al., 1996; Howard and Mendelssohn, 1999a; Howard and Mendelssohn 1999b; Howard and Mendelssohn, 2000; Sanderson et al., 2000; Greiner La Peyre, et al., 2001). Recently, Sanderson et al., (2000) have shown that tidal channels dominate vegetation zonation found in salt marshes of the San Francisco Bay Estuary. This dominance is presumed to be due to hydrologic gradients established by channel geography. However, this dominance was demonstrated without reference to marsh elevations or other physical or biological influences, and

edaphic characteristics were not directly investigated. Closer attention to rooting zone conditions demonstrates the influence of local physical factors on the pattern of vegetation zonation in tidal marsh ecosystems (McKee and Mendelssohn, 1989; Sanchez et al., 1996; Padgett et al., 1998; Brewer et al., 1998 Zedler et al., 1999). Specifically, the influence of factors other than tidal hydrology on vegetation pattern where the physical constraint of salinity tolerance is reduced or temporarily relieved is notable (Smart and Barko, 1978; Pearcy et al., 1982; Ustin et al., 1982; Pearcy and Ustin, 1984; McKee et al., 1989; Callaway et al., 1990; Zedler et al., 1990; Bertness et al., 1992; Shumway and Bertness, 1992; Flynn et al., 1995; Webb and Mendelssohn, 1996; Alvarez-Rogel et al., 1997; Kuhn and Zedler, 1997; Callaway and Zedler, 1998; Ungar 1998; Howard and Mendelssohn, 1999a; Howard and Mendelssohn, 1999b; Alvarez Rogel et al., 2000; Howard and Mendelssohn, 2000; Greiner La Peyre et al., 2001). The emergence of alternative vegetation-structuring influences under conditions of reduced salinity suggests the general importance of soil salinity in determining vegetation zonation. Soil salinities influence vegetation zonation directly by limiting growth, and indirectly by influencing competition, parasitism, and other biotic interactions. We hypothesize that soil salinity gradients structure the vegetation within tidal marshes of the San Francisco Bay/Delta Estuary.

This paper describes some of the relationships between local plant species distributions and the location of tidal channels in San Francisco/San Joaquin Bay/Delta tidal marshes (Figure 1). We conducted vegetation surveys for a system of tidal channels within the First Mallard Branch drainage of Suisun Marsh, CA, and within the Fagan Slough drainage near the Napa River, CA, to match surveys first conducted within the Tule Slough drainage of Petaluma Marsh, CA (previously published). Survey transects were placed perpendicular to first, second and third order channel networks to quantify the distribution of plant species with respect to channel size, local groundwater salinity, and tidal elevation within these drainages.

Methods

Site Descriptions

First Mallard Branch

Observations for this study were made at Rush Ranch, a private property containing approximately 470 ha tidal brackish marsh adjoining the Suisun Marsh complex of marshes along the eastern boundary of Suisun Slough, north of its confluence with Cutoff Slough, Solano County, CA (38°12'30" N, 122°2'30" W). The Rush Ranch marsh site is bounded on the east by the Potrero Hills and on the north by Hill Slough. Local marsh topography is supplied tidally by First Mallard Branch and is part of the Suisun Slough/Montezuma Slough system to the north of Grizzly Bay (Figure 2).

The vegetation at the Rush Ranch study site (hereafter "Rush Ranch") is typical of brackish marshes in the Suisun Marsh complex (Barbour and Major, 1990; Wetland Research Associates, 1990) containing a mixture of species known to occur in typical freshwater to saline marshes (Hickman, 1993; Mason, 1957; Mitsch and Gosselink, 2000). Locally-compiled floras have identified from 56 to 198 species (Grewell, 1997; Wetlands Research Associates, 1990) occurring throughout Rush Ranch, though typically 17-21 species were regularly encountered at the study site within the study time frame (1997-2000). Locally-dominant species include: *Scirpus americanus*, *Lepidium latifolium*, *Scirpus californicus*, *Scirpus acutus*, *Typha angustifolia*, *Distichlis spicata*, *Juncus balticus* and *Grindelia stricta*. A complete list of species encountered during the period 1997-2000 is shown in Table 1.

Fagan Slough

The Fagan Slough Ecological Reserve, a California Department of Fish and Game Area of Special Biological Significance, is located in Napa County, California, USA, adjacent to the Napa River (38°13'28" N, 122°17'30" W). Observations were made within the tidal salt marsh portion of the Reserve, which occupy approximately 97 ha immediately north of Fagan Slough proper, southeast of Steamboat Slough, and west of the Napa County Airport. The marsh is tidally influenced by Fagan Slough, Steamboat Slough, a northern constructed drainage canal, and their smaller tributaries (Figure 3).

The Fagan Slough Ecological Reserve (hereafter “Fagan Slough”) supports tidal salt marsh vegetation typical of the San Francisco Bay Estuary (Barbour and Major, 1990; Hickman, 1993) with approximately 60 species, of which 22 were encountered during this study (Table 2). Locally-dominant species include: *Salicornia virginica*, *Cuscuta salina*, *Scirpus americanus*, *Potentilla anserina*, *Lepidium latifolium*, *Scirpus acutus*, *Distichlis spicata*, *Juncus balticus* and *Scirpus maritimus*.

Tule Slough

A fourth-order tidal channel, Tule Slough is located in the Petaluma Marsh, Marin and Sonoma Counties, California, USA, west of the Petaluma River at Lakeville, CA (38°12'20" N, 122°32'32" W). Complete study site descriptions are described elsewhere (Sanderson et al, 2000). Petaluma Marsh is a saline tidal marsh, bounded primarily on the north, east and south by the Petaluma River, and on the west by hills within the Pacific Coast Range (Figure 4). The Tule Slough study site (hereafter Petaluma Marsh) supports tidal salt marsh vegetation typical of the San Francisco Bay Estuary (Barbour and Major, 1990; Hickman, 1993) with approximately 40 species, of which 13 were encountered during this study (Table 3). Locally-dominant species include: *Salicornia virginica*, *Cuscuta salina*, *Baccharis pilularis*, *Lepidium latifolium*, *Scirpus robustus* and *Spartina foliosa*.

Vegetation Sampling

Vegetation surveys were conducted at each site at approximately peak annual biomass (September/October) within a given year. Transects situated perpendicular to the particular tidal channel of interest were marked and revisited as needed to establish constancy of the dominant local vegetation between seasons and years (for details of surveys at Petaluma Marsh, see Sanderson et al., 2000). For Rush Ranch, 13 transects were established on two adjacent second order channels, and a total of 260 quadrats sampled during 1998, 1999, and 2000. At Fagan Slough, 9 transects were established along two adjacent second order channels totaling 180 quadrats in 1999 and 2000. For comparison purposes, a subset of data from Petaluma Marsh were used (Sanderson, E.W., personal communication) describing 3 transects on three second order channels for 90

sampled quadrats during 1996. Small (0.4m^2) quadrats were used to sample vegetation every meter (0 to 12 m from the tidal channel) or every 5th meter (15 m and beyond) from the tidal channel. Transitions between visually apparent vegetation zones (streamside, transition, and marsh plain) were sampled every meter. Transect length ranged between 25 and 85 meters in order to include the vegetation types typical of the study area. Where continuing transects would involve approaching an adjacent tidal channel, the transect was terminated.

Vegetation cover was estimated using a Braun-Blanquet cover class scheme (Mueller-Dombois and Ellenberg, 1974), and converted to cover class mid-point values for analysis. Total cover values for a given quadrat location were allowed to exceed 100% in order to include multiple-level canopy vegetation structure.

Channel Characterization

Channels were characterized using a channel order scheme based upon bifurcation junctions (Horton, 1945; Leopold 1953; Myrick 1963; Strahler, 1964). Additionally, cross-sectional areas of channels using width and depth measurements were computed for comparison within and across different sites. Table 4 lists selected cross-section areas from each marsh as an example of the size of tidal channels within the study sites. Channels at Fagan Slough are 3rd order, and channels at Rush Ranch are 1st order.

Elevation Measurements

Elevations were measured using locally-installed benchmarks, triangulated for stability. Elevation surveys were conducted to establish local elevations using a standard stadia rod (marked in 100^{ths} of feet) and a commercial-grade level (Topcon AT-G7 Autolevel©). Benchmarks were reoccupied and reexamined each year of the survey to confirm stability. Elevations were read to the nearest 2.5×10^{-4} ft, and survey closure obtained in the field was maintained at 0.05 feet (± 3 mm). Any turning point not closed to within this value was discarded and resurveyed. All field measurements were converted to metric units after collection for analysis and reporting.

Salinity Measurements

Stillwells for collecting soil pore water for salinity measurements were installed within each vegetation zone, generally 1.0, 10.0, and 30.0 meters from the nearest tidal channel. Stillwells were constructed of 3/4" (1.9 cm) PVC pipe, in 25 cm lengths. Perforations in each pipe were made for collection of pore water at a depth of 15 cm below the ground surface, a depth that was verified to be within the local active rooting zone. Caps were applied to each end of the well to prevent leakage. Nests of three to five wells were grouped at a given location, and measurements were averaged for each location. Quarterly salinity measurements were collected in order to describe any seasonal changes in the rooting zone due to tidal action or precipitation. Total salinity readings were made using a handheld salinity refractometer (Sper Scientific). Samples were handled in the field using clean plastic tubing, washed between each use with deionized water.

Data Analysis

Vegetation data were analyzed using STATVIEW© ANOVA and regression techniques (SAS Institute, 5.0.1 for Macintosh, 1998). Significance was set at $\alpha = 0.05$. Vegetation species were selected for analysis based upon degree of cover dominance (visual and statistical) within each quadrat and within each marsh. Only species with percent cover recorded as 20% or greater for a given location were included. Species percent cover (as the average for a given distance from the nearest tidal channel) was correlated with measured physical variables (elevation, soil salinity, distance from tidal channel, and distance from tidal source). Comparison of results between marshes was then conducted to determine the general response by common or equivalent species to the major physical gradients encountered.

Results

Interannual variation in vegetation surveys was minimal. Student's *t* tests of species percent cover by transect show few significant differences between years (Table 5). Where there were differences, only changes in species' patch size was noted, particularly in response to disturbances on the marsh surface (see below), or to expansion

of *Scirpus americanus* at Rush Ranch, in particular. To eliminate any unknown potential sources of interannual error in comparison between Rush Ranch and Fagan Slough, vegetation surveys from 1999 are used henceforth for both marshes. Comparison to Petaluma Marsh is between vegetation data collected primarily in 1996, but supplemented with updated physical and vegetation measurements where noted.

Rush Ranch

Correlation between species percent cover and elevation was low (mean $r^2=0.019$). In cases where elevation was found to be a significant factor in explaining variance of percent cover ($p < 0.0001$), regression analysis did not reveal strong explanatory ability using elevation as an independent variable (Table 6). Most species occupy a significant portion of the marsh elevations surveyed (20 – 30 cm range), and do not show tendency to occupy areas with specific elevational requirements (Figure 5). Exceptions to this pattern can be seen in two species (*Glaux maritima* and *Grindelia stricta*), which are uncommon within the survey site. Analysis of *Scirpus americanus* and *Juncus balticus* are representative of survey results, and are shown in Figure 6. Each of these species occupies a range of elevations spanning 40 cm and 30 cm, respectively, of the total marsh surface surveyed (44 cm extent in total). *Scirpus americanus* shows dominance (50% canopy cover or more) throughout its elevational range, while *Juncus balticus* is dominant mainly at higher elevations. These characteristics are consistent with field observations that *Scirpus americanus* is an aggressively-growing species, both streamside and in areas with sufficient moisture on the marsh plain, while *Juncus balticus* is a robust, stable occupant of the “higher, drier” transitional regions of the marsh, if able to occupy less optimal areas without showing dominance.

A summary of all species’ cover values by position is shown in Figure 7. Apparent from this summary are several observations: 1) a streamside zone of dominance is present between 0 m and 25 m from the tidal sloughs. This zone includes *Scirpus americanus*, *Typha angustifolia*, *Convolvulus arvensis*, and *Potentilla anserina*; 2) *Juncus balticus* is dominant (the species showing the highest percent cover) in the intermediate, transitional, zone between distances of approximately 25 m and 70 m from the channels, and; 3) *Distichlis spicata* is dominant beginning at approximately 70 m

from the channels. These changes in vegetation dominance are apparent despite no abrupt changes in elevation profile (Figure 8).

Correlation of species percent cover with distance from channel was low (mean $r^2=0.179$), but in all but one case (*Grindelia stricta*) higher than for elevation (Table 6). This result is consistent with Sanderson et al. (2000) in that predictability in vegetation cover due to distance from channels is found to be important in determining the nature of the tidal marsh landscape at Rush Ranch. Streamside species (*Scirpus californicus*, *Scirpus acutus*, *Typha angustifolia*) show the strongest zonation consistent with their affinity for water, but most species occur over a wider range of distances (Figure 9). Changing cover values of species within their respective ranges are important to note (Figure 7), and are discussed in more detail below (see D_{75} criterion). It is likely that species are showing productivity responses to moisture and/or salinity gradients within the soil column across the landscape (Foin et al., 2000; Culberson and Foin, in review) as well as demonstrating the boundaries of their realized niches under competition for light and nutrient resources. ANOVA and regression results are presented in Figure 10 for *Distichlis spicata* and *Juncus balticus* as examples of species with stronger cover predictability using distance from channel. These examples show that predictability in percent cover for a given species can be made using distance from tidal slough as an independent variable at Rush Ranch (r^2 between 0.4 and 0.5).

Incorporating distance from tidal source (transect location relative to the origin of tidal incursion, First Mallard Branch) does not improve the regression developed for distance from tidal sloughs, and has been eliminated from further analysis. This lack of importance of distance from tidal source in regressions, however, does reiterate the importance of local tidal geography (expressed as smaller order channels) identified by Sanderson et al. (2000).

Measurements of soil pore water show an overall pattern of increasing salinity with increasing distance from tidal channel, and variable salinity in the transition zone (Figure 11). This pattern was consistent over the duration of the surveys, though marsh-wide increases in salinity are apparent as winter/spring precipitation abates. The non-linear pattern of soil salinity increase with distance from channel is important since it implies that vegetation zonation would best be examined by non-linear relationships

which include soil salinity as well as (or instead of) distance from channel. We successfully incorporate a non-linear method of characterizing vegetation distributions with regard to distance from channels using the D_{75} criterion (discussed below). Using the D_{75} criterion we find that vegetation zonation can be explained in terms of soil salinity across all examined marshes regardless of linear distance from channel. This is a significant finding, since the relationship of soil salinity to distance from channel depends largely upon where in the Estuary the relationship is determined.

Fagan Slough

Correlations between elevation and species percent cover are small (mean $r^2=0.112$), but higher than at Rush Ranch (compare Tables 6 and 7). This reflects the fact that mean elevations at Fagan Slough are on average 40 cm higher than at Rush Ranch (Figure 12), resulting in an increase in influence of physical conditions associated with higher elevation (less local over marsh flooding, lower water availability, and higher soil salinities). Similar to Rush Ranch, regressions of species' cover on elevation are largely not significant (Table 7). Species encountered at Fagan Slough occur over a wide range of the elevational profile described, and except for *Distichlis spicata* (which is uncommon) and *Cuscuta salina* (a hemiparasite found within stands of *Salicornia virginica*), are not determined by elevation (Figure 13). Typical results from ANOVA and regression analysis for *Salicornia virginica* and *Distichlis spicata* are shown in Figure 14. *Salicornia virginica* shows highest cover value at higher elevations within its range, as is expected for a species with noted tolerance to higher soil salinities. *Distichlis spicata* also shows some tolerance to salt, but while restricted to the upper range of elevations encountered is uncommon in a *Salicornia virginica*-dominated marsh plain landscape.

Correlation of species' percent cover with distance from tidal slough was also low (mean $r^2=0.069$, see Table 7). This is surprising, since at Petaluma Marsh, where physical conditions are more similar to Fagan Slough than at Rush Ranch, recent research has identified strong correlation of percent cover with linear distance from tidal slough (Sanderson et al., 2000). However, soil salinities at Fagan Slough, while higher than at Rush Ranch, do not rise as rapidly with distance from channel as those at Petaluma

Marsh (see below). This result suggests that the strong relationship found between plant species' cover and distance from slough at Petaluma Marsh is due primarily to the presence of strong salinity gradients in the near-stream environment. We expected a similar relationship between species' cover and distance from channel at Fagan Slough, but the weaker soil salinity gradient with distance from slough prevented this finding. This result is consistent with lower incoming tidal salinities at Fagan Slough compared to Petaluma Marsh.

Species zonation with respect to distance from channel at Fagan Slough shows some pattern in the data collected (Figure 15), but generally the relationship is not apparent. Results from ANOVA and regression analysis for *Scirpus americanus* and *Distichlis spicata* are shown as examples in Figure 16, and regression r^2 summaries are provided in Table 7. Direct correlation of canopy dominance with distance from channel is not indicated, which would be the case if strong linear gradients in soil physical conditions were present. Streamside species (*Lepidium latifolium*, *Scirpus americanus*, *Scirpus acutus*) show affinity to more streamside positions, transition species (*Juncus balticus*) for transitional positions, and marsh plain species (*Salicornia virginica*, *Cuscuta salina*) for marsh plain positions, but these relationships are not exclusive (Figure 17). As at Rush Ranch, species are found at a wide range of distances from the tidal channels. This pattern is found despite the smooth but increasing elevation gradient with distance surveyed at Fagan Slough (Figure 18). The one break in this elevation gradient noted between 35 m and 55 m (a local depression, representing an actively-eroding first-order channel on the marsh) is matched by an abrupt cover increase in a streamside species (*Scirpus maritima*), but does not help to separate the influences of elevation and distance from channel – both characteristics provide additional available water to which *Scirpus maritima* is responding.

Closer inspection of these data, however, reveal that species' cover distribution relationships (using the D_{75} criterion, see below) with distance are evident. Cumulative percent cover values by species with distance from tidal sloughs reveal positional differences in species cover dominance across the marsh landscape – see the area depicted for *Distichlis spicata* from 5.0 to 25.0 meters from the tidal slough in Figure 16, for example. In other words, if each species is considered relative to its own total cover

value across the marsh surface, positional relationships depending upon distance from tidal channels are found.

Analysis incorporating distance from the tidal source at Fagan Slough (the Napa River) does not add any additional explanation.

Soil pore water salinity shows a pattern of increasing salts with distance from the tidal slough (Figure 19). These soil salinities are on average two to four times what is found at Rush Ranch across the zones indicated (Figure 11), reflecting the difference in average salinities found in incoming tidal water supplies (2-5 ppt at Rush Ranch versus 15-17 ppt at Fagan Slough). In the one location showing departure from the pattern of increasing salinities shown in Figure 19, soil pore water salinities decrease as an adjacent tidal slough is approached (Marsh Plain position, 115.0 m). This is important in that it demonstrates the dependence of soil pore salinity on the presence of tidal channels and water movement within the soil column even in areas of higher local elevation.

Petaluma Marsh

Previous work demonstrated that plant assemblages in Petaluma Marsh show distribution patterns that reflect the influence of tidal channel networks (Sanderson et al., 2000). These patterns are argued to be related to the delivery and drainage of water to and from the tidal marsh plain. The strongest evidence for this relationship is shown in Sanderson et al. (2001), where vegetation and tidal channels are related by assigning 'influence weights' to channels based on size and position relative to the vegetation and predicting what the expected vegetation cover should be. Correlation of vegetation percent cover to elevation and soil pore water salinity is not precisely known from previous published reports. Researchers familiar with the Tule Slough study site suggest that these relationships are similar to those found at Rush Ranch and Fagan Slough (J.N. Collins, unpublished data). Moderate to strong correlation of plant species' percent cover with elevation and position relative to the tidal channels has been observed (Sanderson et al., 2000; J.N. Collins, unpublished data). Soil pore water samples collected previously at Petaluma Marsh shown the same pattern of increasing salinity with distance from the tidal channel (Figure 20a). Limited salinity measurements collected for the purposes of this study also support these findings (Figure 20b). Soil salinity sample data from

Petaluma Marsh reflect the fact that incoming tidal water is more seasonably variable over the course a year (7-10 ppt during spring runoff periods, 25-35 ppt during summer drought periods), and that marsh plain locations can experience very high local soil salinities (100 ppt or more) due to higher summer tidal salinities and limited overmarsh flooding, compared to either Fagan Slough or Rush Ranch. These factors combine to produce salinity gradients that are stronger than at Fagan Slough or Rush Ranch, and vegetation zonation is more compressed as a result (Sanderson et al, 2000; and see below).

Between Marsh Comparisons

The lack of strong linear relationships between tidal marsh vegetation and distance from tidal marsh channels or soil surface elevation within a given marsh is surprising, especially given the visual appearance of zonation within a given marsh landscape. When species of each of the visually evident vegetation zones (streamside, transition, and marsh plain) are considered with regard to their individual degree of dispersion from the nearest tidal channel (which includes extent of cover as well as relative cover value), a general pattern of vegetation zonation emerges. This pattern is especially evident when considered across all of the tidal marshes studied, and brings to light the influence of regionally-variable soil salinity as an important physical determinant of vegetation zonation, irrespective of other physical variables. Species are found to occur over a range of soil moistures, soil surface elevations, and positions relative to nearby tidal channels, but those ranges appear to have realized limits in the landscape, and produce vegetation zones that reflect the interaction of moisture availability and regional soil salinity. For this reason, when we compare the vegetation zonation at each of the described marshes, we find that increasing salinity of tidal waters in the downstream direction of the San Francisco Bay/Delta Estuary is reflected in the compression in the distribution of species associated with tidal channels, and in the channel-ward displacement of the transition zone found between the streamside and marsh plain species.

A dispersion criterion was established, termed “75% cover distance,” or D_{75} , which describes the distance from a tidal channel necessary to travel in order to encounter

75% of the cover of a given species along a given transect. In other words, in traversing from the tidal channel to the D_{75} an observer will have encountered 75% of the cover of a given species extant on that transect. The 75% cover value was chosen to provide an adequate estimation of where the majority of a species' distribution is found without being so inclusive as to obscure the underlying relationship (as in Figures 9 and 15). An example of the 75% cover distance relationship (points are mean values for all transects) is presented for *Juncus balticus* at Rush Ranch in Figure 21, and includes a fitted polynomial to assist visualization. For comparison, Table 8 lists the D_{75} criteria for representative species for each of the major vegetation zones in each of the studied marshes. The data for this table are presented in Figure 22. These data display several important characteristics which accurately describe the vegetation surveyed: 1) vegetation zones (streamside, transition, and marsh plain) of characteristic plant species located relative to the position of tidal channels are evident in the marshes described; 2) the distance to the D_{75} point of species typifying these vegetation zones decreases with downstream location within the Bay/Delta Estuary, and; 3) when moving downstream within the Bay/Delta Estuary, progressively more of each marsh surface is occupied by one halophytic species (*Salicornia virginica*) which is known to be highly tolerant of saline conditions in the absence of prolonged tidal submersion, often forming virtual monocultures in areas few other emergent macrophytes can survive.

Using these data, a generalized pattern of vegetation zonation was developed for marshes within the San Francisco Bay/Delta Estuary (Figure 23). The strength of the association between vegetation and tidal channels is stronger as one moves from freshwater/brackish to euryhaline conditions. The width of the streamside zone decreases, the position of the transition zone moves closer to the tidal channel, and the overall extent of the marsh plain zone expands as ocean salinities are approached. This phenomenon is apparent from an evaluation of aerial photography (Culberson, unpublished data), and has been utilized successfully to develop predictions of individual species distributions for a marsh within 40 km of the Golden Gate (Sanderson et al., 2001). Similar predictability has not been demonstrated in upstream marshes where soil salinities do not impose such a tight correlation between tidal marsh vegetation and tidal channel position.

Changes in regional tidal salinity correlate well with the generalized vegetation pattern outlined above. The marshes described above are located along the hydrologic gradient extending from the confluence of the Sacramento and San Joaquin Rivers to San Francisco Bay. This gradient includes salinity ranges from freshwater/brackish (< 5 ppt in Suisun Marsh) to brackish-saline (between 10 and 25 ppt near bayward reaches of the Napa River) to saline conditions (> 30 ppt in Petaluma Marsh and San Pablo Bay). Representative summer soil salinities for each of the studied marshes are shown in Figure 24. Soil pore water salinities at a distance of 1.0 m from the tidal slough are identical to those found in water circulating in the tidal channels themselves at the time of sampling.

Even though elevation should contribute drainage, limit flooding frequency and elevate local soil salinity, soil surface elevations played little direct role in the zonation of species encountered, either locally or regionally. Exceptionally low local elevations do tend to be colonized by only streamside species, but those elevations occur only within the streamside zone. Higher elevations are occupied by more salt-tolerant species in all three marshes, but the correlations between elevation and species identity are low (Tables 6 and 7). Comparison across marshes show that elevations at Rush Ranch and Fagan Slough can differ by as much as 40 cm or more (Figure 12), but species lists of plants found within these marshes overlap significantly (Tables 1, 2, and 3). It is our view that elevation is a poor predictor of tidal marsh vegetation zonation. Soil pore water salinity is a more useful physical parameter when describing the nature of local and regional zonation in tidal marsh vegetation.

Discussion

Our understanding of the character of vegetation in tidal marshes in the San Francisco Bay/Delta is that as one moves downstream toward the Pacific Ocean the vegetation changes from freshwater-dominated to halophyte-dominated communities: *Scirpus acutus* and *Typha latifolia* give way to *Scirpus americanus*, and *Juncus balticus*, and eventually to *Frankenia salina* and *Salicornia virginica*. This pattern is found along the gradient from streamside to marsh plain as well: less salt-tolerant *Scirpids* are replaced by *Juncus balticus* and *Distichlis spicata*, with *Salicornia virginica* dominating areas most distant from tidal channels. The range over which this secondary pattern

occurs depends on where in the regional salinity gradient a marsh is located – further upstream the pattern is spread out over longer distances than downstream (70 meters in Suisun Marsh versus 3 meters at Petaluma Marsh). The proximate cause of these patterns has not been previously identified. Vegetation zonation has been shown in response to a few physical factors: water availability (Eleuterius and Eleuterius 1979; Ustin et al., 1982; Vince and Snow, 1984a; Vince and Snow, 1984b; Bridgeham and Richardson, 1993; Webb and Mendelssohn, 1996; Haltiner et al., 1997; Kuhn and Zedler, 1997; Hunt et al., 1999), sulfides (McKee and Mendelssohn, 1989; Flynn et al., 1995; Burdick et al., 1989), and disturbance (Wilson and Keddy, 1986; Brewer et al., 1998). Soil salinity has frequently been determined to play a role in marsh vegetation zonation in other parts of North America and Europe (Percy et al., 1982; Zedler and Beare, 1986; Pezeshki et al., 1987; Earle and Kershaw, 1989; McKee and Mendelssohn, 1989; Callaway et al., 1990; Kenkel et al., 1991; Shumway and Bertness, 1992; Bertness and Hacker, 1994; Flynn et al., 1995; Webb and Mendelssohn, 1996; Wilson et al., 1996; Callaway and Zedler, 1998; Howard and Mendelssohn, 1999a; Howard and Mendelssohn, 1999b; Alvarez Rogel et al., 2000; Howard and Mendelssohn, 2000; Greiner La Peyre et al., 2001). In most cases, one or more species performs physiologically better under given salinity conditions than other species, and this performance results in local dominance.

Foin et al. (2000), point out that whatever the underlying cause of vegetation zonation along the salinity gradient from the Delta to the Pacific Ocean, it is due to the relative productivity of tidal marsh plant species occupying these zones. Higher productivity (dominance) depends upon location within existing salinity gradients. Given local spatial variability in physical conditions within the larger salinity gradient, the identity of plant species at a particular location will vary from time to time. Species that are more tolerant of sustained “marginal” growth conditions (*Salicornia virginica* in high salt environments, for example) will dominate in locations where “marginal” conditions are the norm. Species that show high productivity under “optimal” conditions (*Scirpus californicus* in freshwater, flushed environments) will dominate in wetter years and in more frequently flushed locations. Longer-term stability of *Salicornia virginica* within upper marsh plains has been remarked as a feature of Bay/Delta marshes (Wells and Anderson, 1995; Ingram et al., 1996; Goman and Wells, 2000), while productivity in tule

stands (*Scirpus* spp.) can vary considerably year to year with runoff and precipitation (Culberson, personal observation). Local soil salinity, mediated through tidal hydrology, controls local vegetation productivity, and determines vegetation zonation in marshes of the San Francisco Bay/Delta (Culberson and Foin, in review). In the present study, we determine that local rooting zone soil salinity underlies the regional pattern of dominance in vegetation zonation found in tidal marshes of the Bay/Delta Estuary.

Acknowledgements

The authors would like to thank the U.S. Fish and Wildlife Service, the California Department of Fish and Game, and the Solano County Farmlands and Open Space Foundation for permission and access to study sites described in this paper. Josh Collins, Mary McNally, Walter Pavlich, Hank Williams, Brenda Grewell, Mary Pakenham-Walsh, and Renee Spenst, provided valuable field assistance. Kevin Gibson provided useful advice during the conduct of this project. This paper is funded by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA66RG0477, project number R/CZ-154 through the California Sea Grant College System, and in part by the California State Resources Agency. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies. The U.S. Government is authorized to reproduce and distribute for governmental purposes.

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Personal Communication

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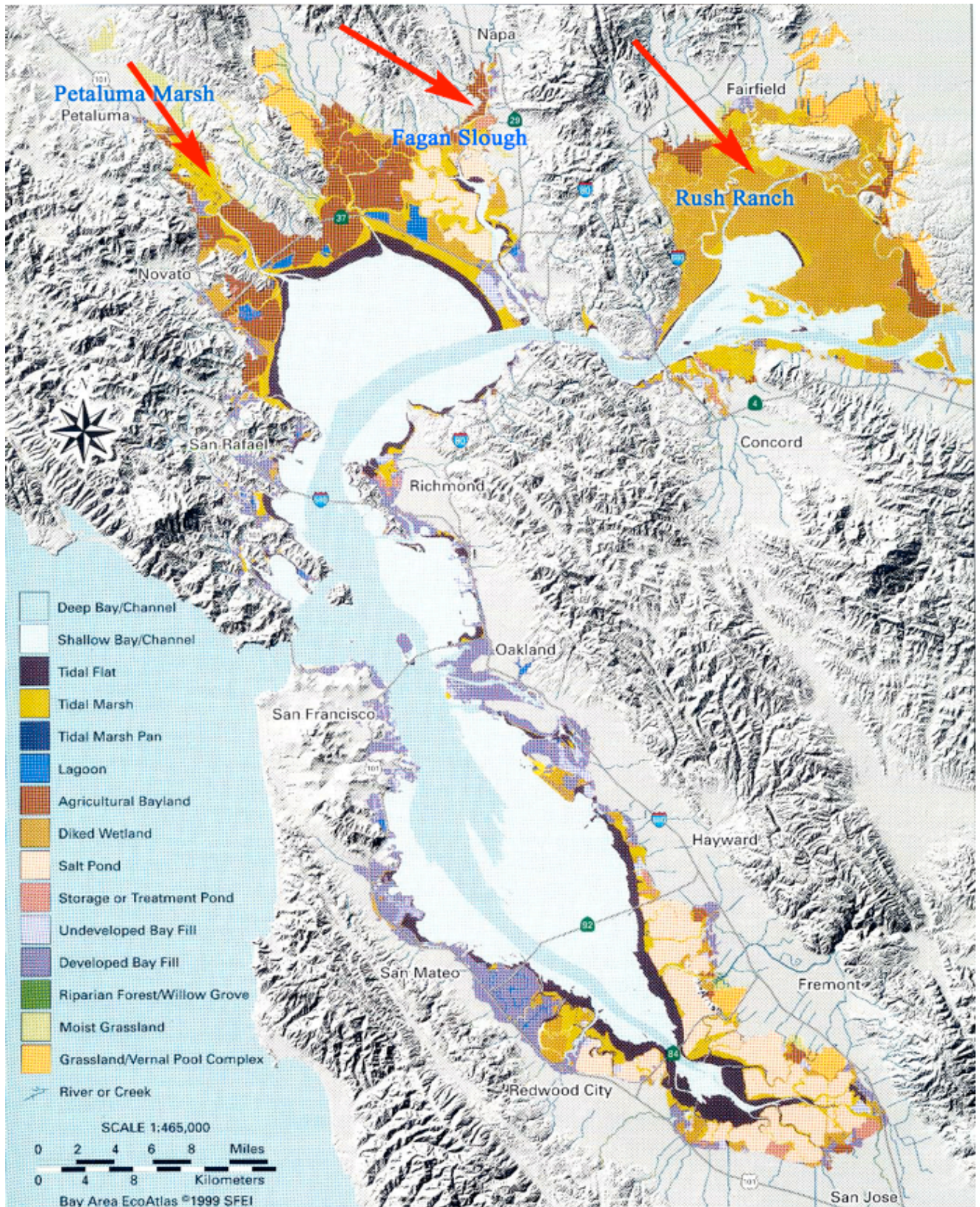


Figure 1. Map showing location of Study sites, California, USA.



Figure 2. Map of First Mallard Branch Area/Rush Ranch, Solano County, CA, USA.



Figure 3. Map of Fagan Slough Ecological Reserve, Napa County, CA, USA.

Figure 4. Map of Tule Slough Area/Petaluma Marsh, Sonoma County, CA, USA.

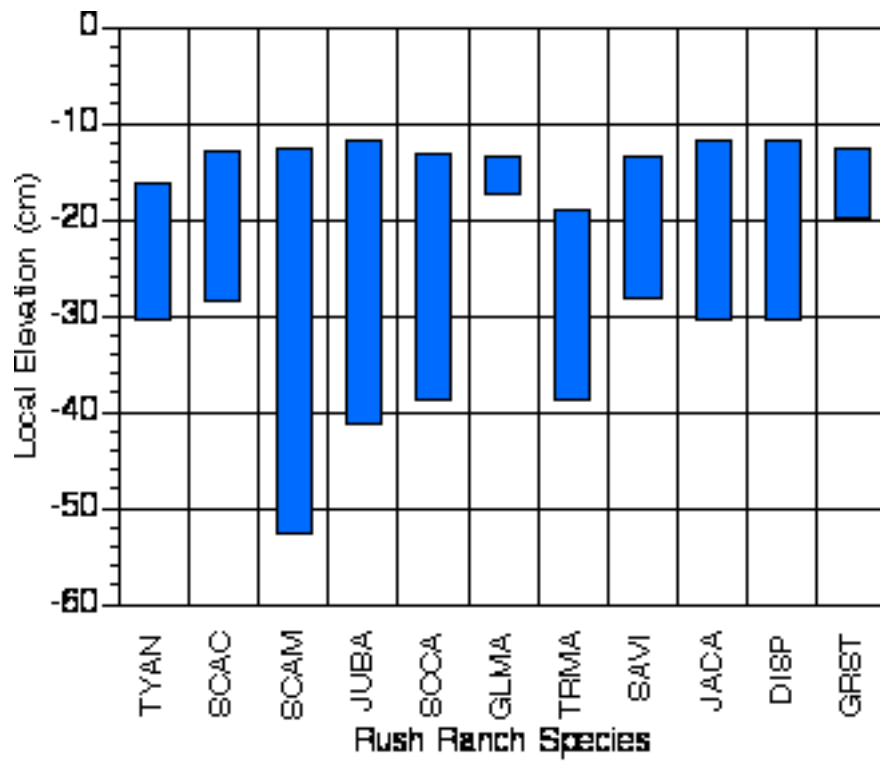
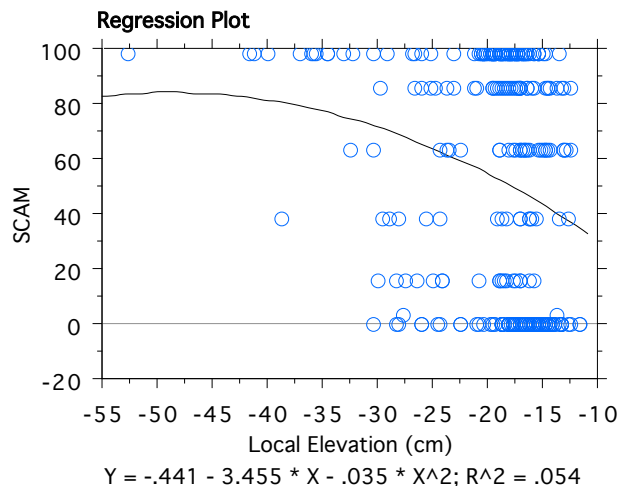


Figure 5. Species presence versus elevation range for quadrats collected at Rush Ranch.

**Regression Summary
SCAM vs. Local Elevation (cm)**

Count	282
Num. Missing	16
R	.232
R Squared	.054
Adjusted R Squared	.047
RMS Residual	41.444

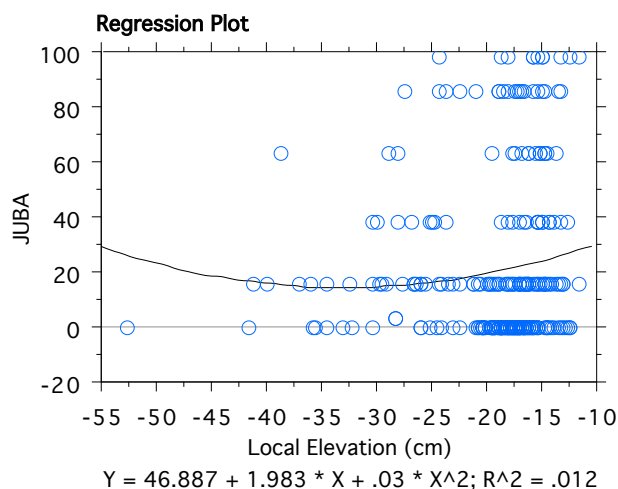


**ANOVA Table
SCAM vs. Local Elevation (cm)**

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	2	27242.274	13621.137	7.930	.0004
Residual	279	479221.890	1717.641		
Total	281	506464.164			

**Regression Summary
JUBA vs. Local Elevation (cm)**

Count	282
Num. Missing	16
R	.108
R Squared	.012
Adjusted R Squared	.005
RMS Residual	29.559



**ANOVA Table
JUBA vs. Local Elevation (cm)**

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	2	2890.058	1445.029	1.654	.1932
Residual	279	243774.602	873.744		
Total	281	246664.660			

Figure 6. ANOVA and Regression Summaries for Rush Ranch using *Scirpus americanus* (SCAM) and *Juncus balticus* (JUBA) versus elevation.

Figure 7. Vegetation Survey showing species' mean cover value by position at Rush Ranch.

Figure 8. Mean elevations by transect location at Rush Ranch.

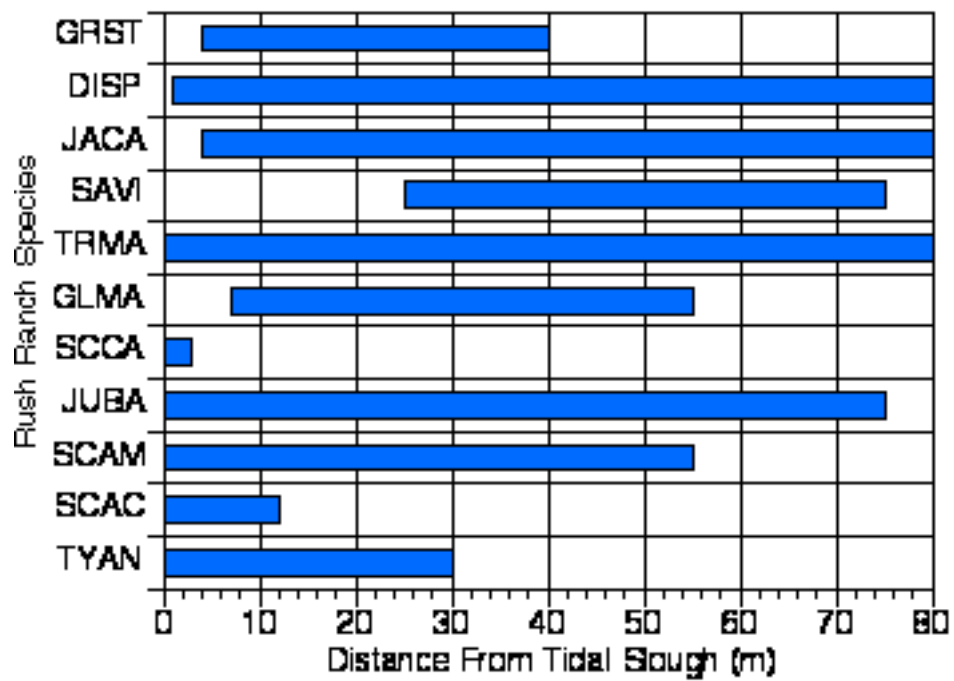
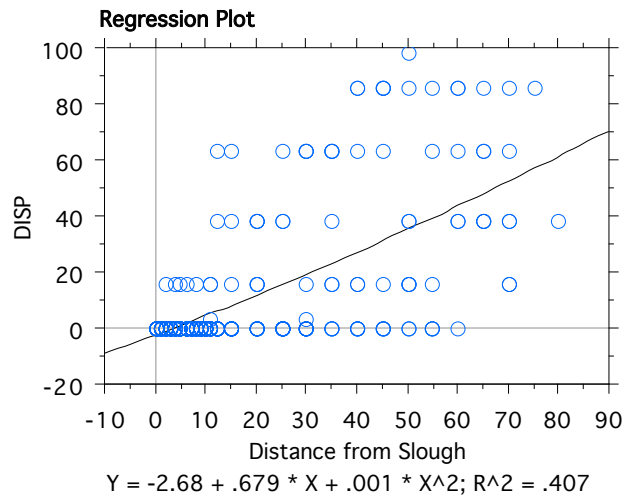


Figure 9. Species presence versus distance from tidal sloughs for quadrats at Rush Ranch.

Regression Summary
DISP vs. Distance from Slough

Count	282
Num. Missing	16
R	.638
R Squared	.407
Adjusted R Squared	.403
RMS Residual	18.237

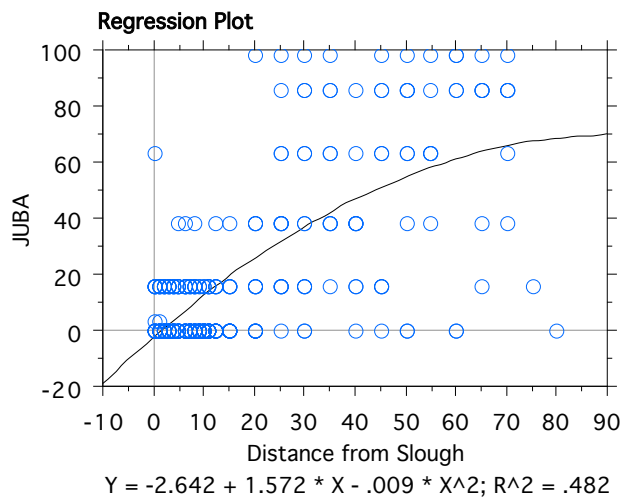


ANOVA Table
DISP vs. Distance from Slough

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	2	63749.005	31874.503	95.838	<.0001
Residual	279	92791.992	332.588		
Total	281	156540.997			

Regression Summary
JUBA vs. Distance from Slough

Count	282
Num. Missing	16
R	.694
R Squared	.482
Adjusted R Squared	.478
RMS Residual	21.409



ANOVA Table
JUBA vs. Distance from Slough

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	2	118780.624	59390.312	129.570	<.0001
Residual	279	127884.036	458.366		
Total	281	246664.660			

Figure 10. ANOVA and Regression summaries for Rush Ranch using *Distichlis spicata* (DISP) and *Juncus balticus* (JUBA) versus distance from tidal slough.

Figure 11. Quarterly soil pore water salinities, Rush Ranch, 2000-01.

Figure 12. Average elevation profiles for vegetation transects at Rush Ranch and Fagan Slough (calibrated using slack high tide).

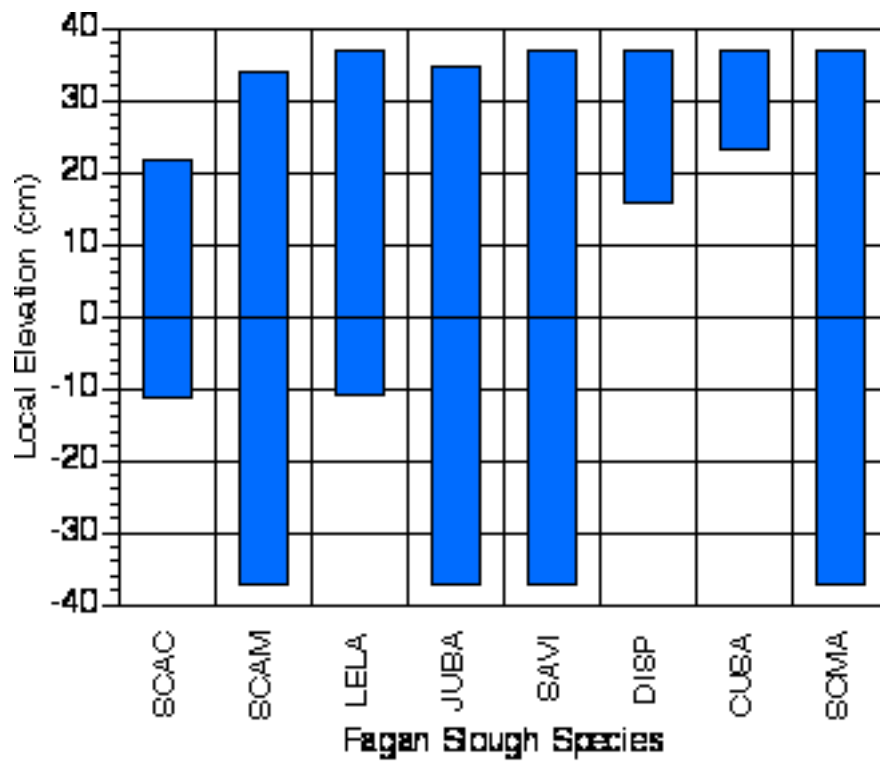
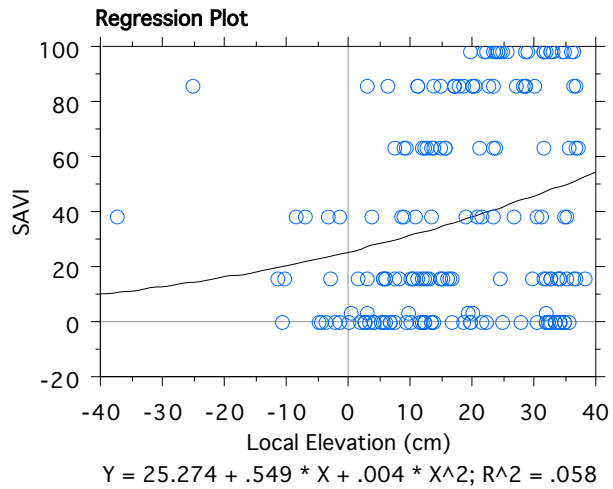


Figure 13. Species presence versus elevation range for quadrats collected at Fagan Slough.

Regression Summary

SAVI vs. Local Elevation (cm)

Count	182
Num. Missing	8
R	.242
R Squared	.058
Adjusted R Squared	.048
RMS Residual	36.358



ANOVA Table

SAVI vs. Local Elevation (cm)

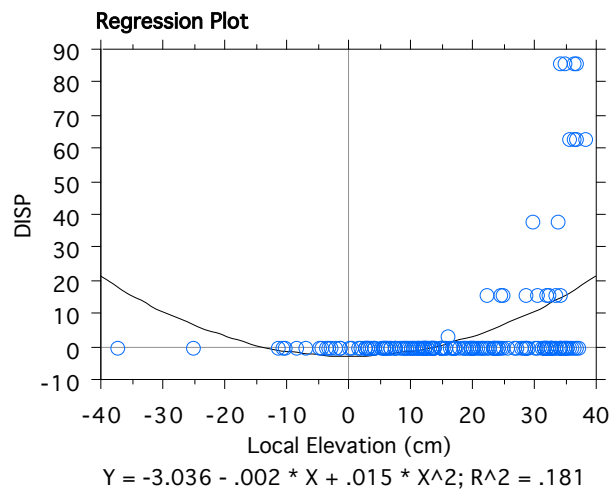
	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	2	14656.824	7328.412	5.544	.0046
Residual	179	236623.145	1321.917		
Total	181	251279.968			



Regression Summary

DISP vs. Local Elevation (cm)

Count	182
Num. Missing	8
R	.426
R Squared	.181
Adjusted R Squared	.172
RMS Residual	14.590



ANOVA Table

DISP vs. Local Elevation (cm)

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	2	8445.744	4222.872	19.838	<.0001
Residual	179	38103.274	212.867		
Total	181	46549.018			

Figure 14. ANOVA and Regression Summaries for Fagan Slough using *Salicornia virginica* (SAVI) and *Distichlis spicata* (DISP) versus elevation.

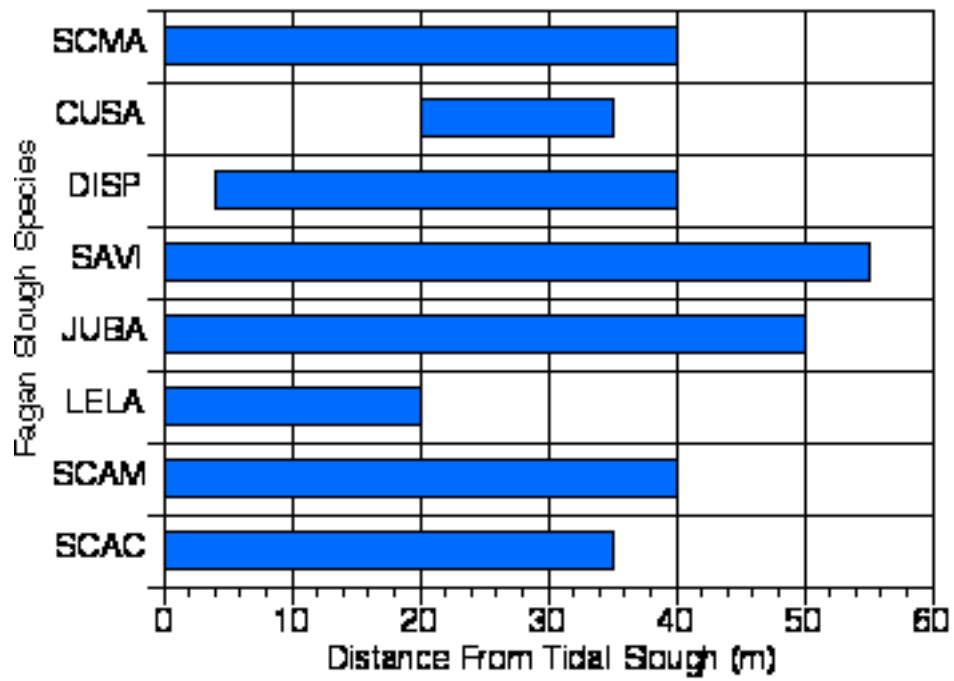
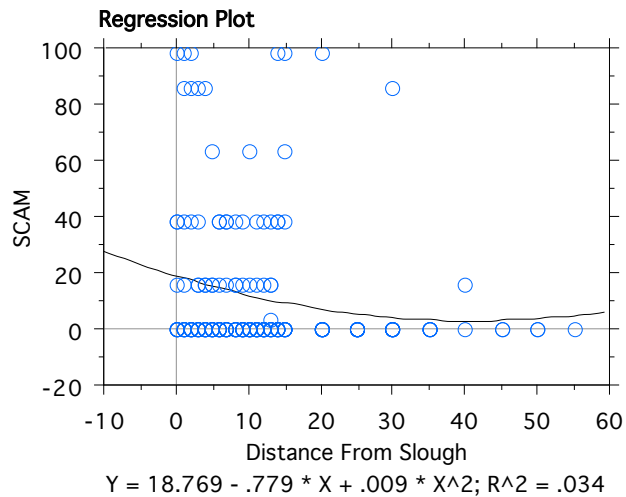


Figure 15. Species presence versus distance from tidal sloughs for quadrats at Fagan Slough.

**Regression Summary
SCAM vs. Distance From Slough**

Count	182
Num. Missing	8
R	.184
R Squared	.034
Adjusted R Squared	.023
RMS Residual	24.351

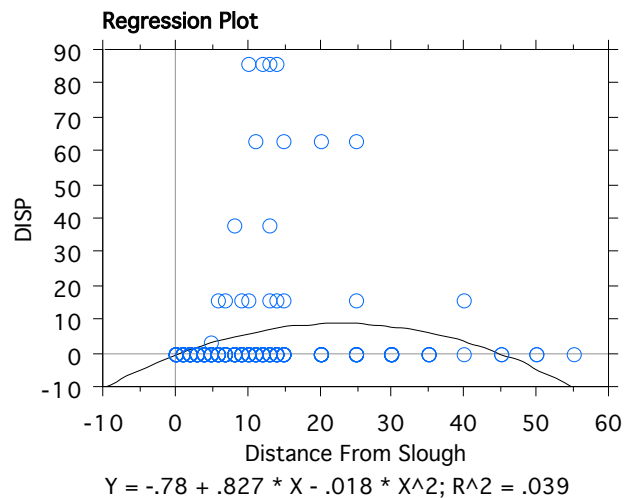


**ANOVA Table
SCAM vs. Distance From Slough**

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	2	3714.178	1857.089	3.132	.0460
Residual	179	106138.701	592.954		
Total	181	109852.879			

**Regression Summary
DISP vs. Distance From Slough**

Count	182
Num. Missing	8
R	.198
R Squared	.039
Adjusted R Squared	.028
RMS Residual	15.807



**ANOVA Table
DISP vs. Distance From Slough**

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	2	1823.600	911.800	3.649	.0280
Residual	179	44725.418	249.863		
Total	181	46549.018			

Figure 16. ANOVA and Regression summaries for Fagan Slough using *Scirpus Americanus* (SCAM) and *Distichlis spicata* (DISP) versus distance from tidal slough.

Figure 17. Vegetation survey showing species' mean cover value by position at Fagan Slough.

Figure 18. Mean elevations by transect location at Fagan Slough.

Figure 19. Quarterly soil pore water salinities, Fagan Slough, 2000-01.

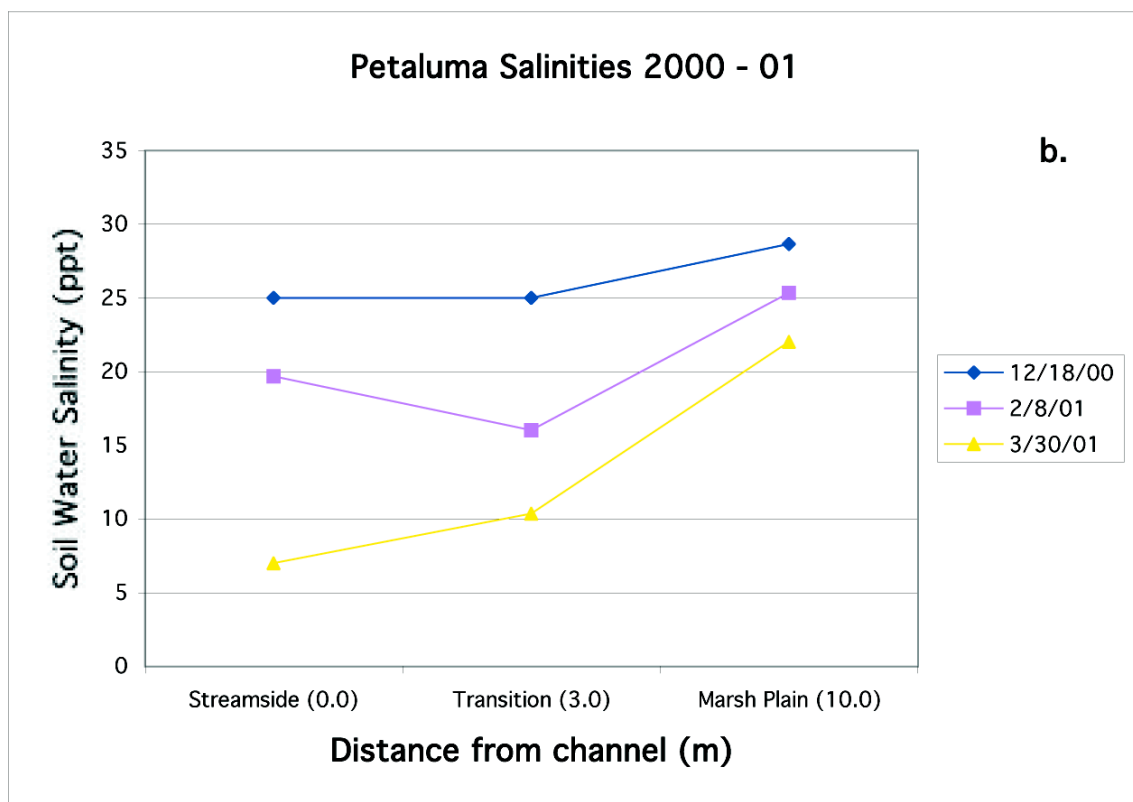
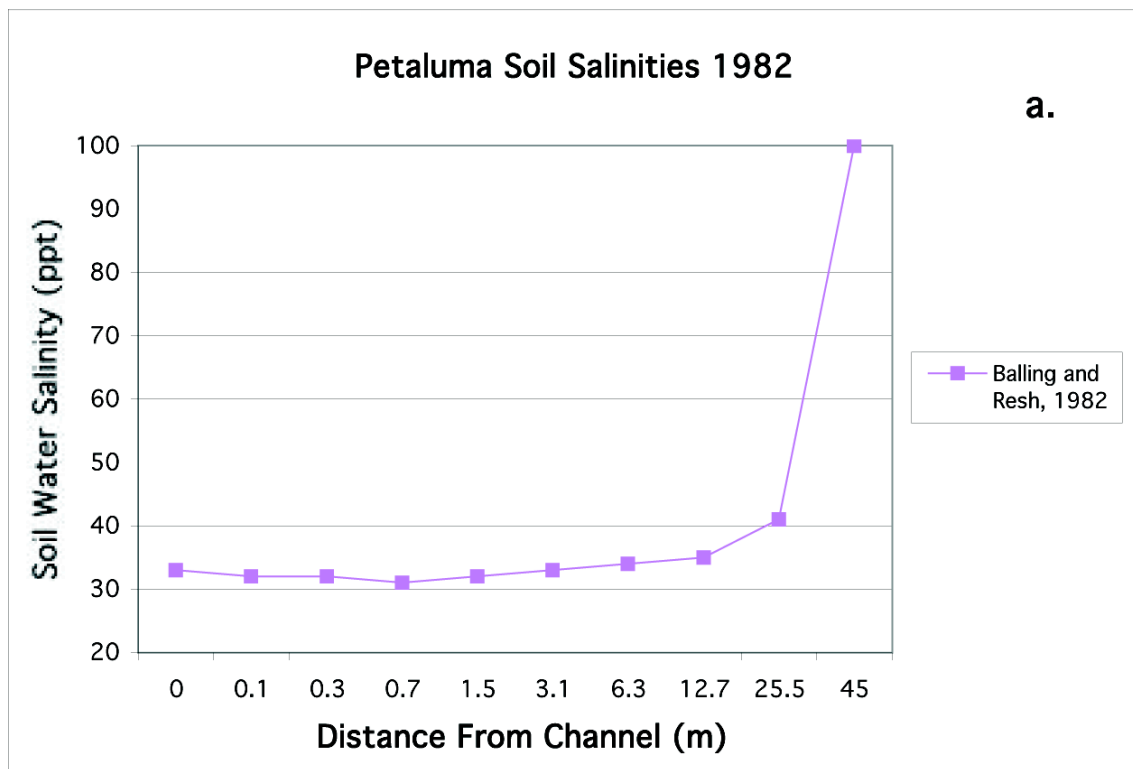


Figure 20. Soil pore water salinities, Petaluma Marsh.
 a. from Balling and Resh, 1982.
 b. current study.

Figure 21. D_{75} criterion for *Juncus balticus* at Rush Ranch.

Figure 22. Data and D_{75} criteria from three tidal marshes in the San Francisco Bay/Delta Estuary, CA. Plot lines added to aid visualization.

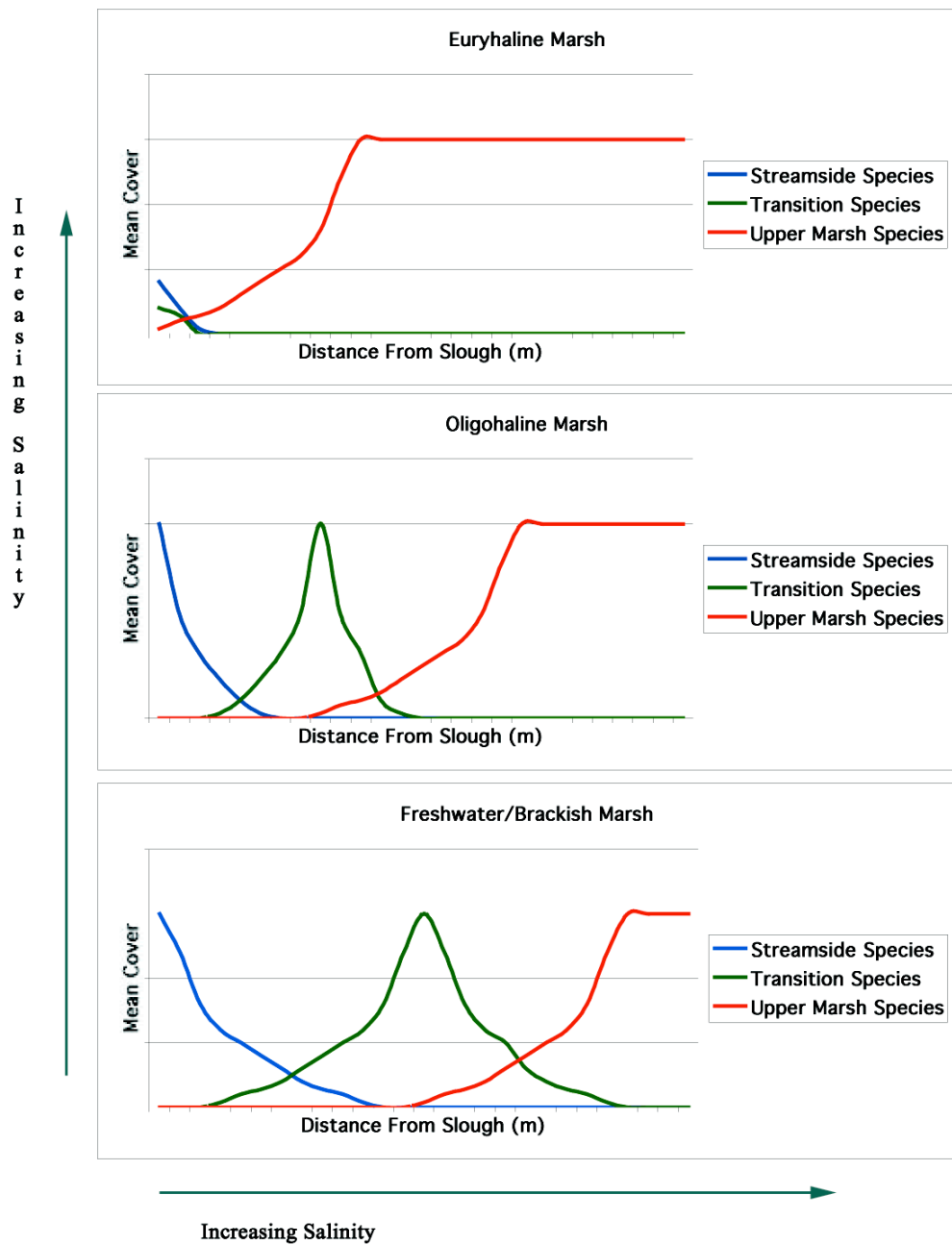


Figure 23. Generalized vegetation pattern for marshes of increasing salinity, including within-marsh gradients of increasing salinity.



Figure 24. Summer 2000 soil pore water salinities for Rush Ranch, Fagan Slough, and Petaluma Marsh.

Table 1. List of species encountered at Rush Ranch, 1997-2000.

Species name	Coded Name
<i>Apium graveolens</i>	APGR
<i>Aster chilensis</i>	ASCH
<i>Atriplex triangularis</i>	ATTR
<i>Convolvulus arvensis</i>	COAR
<i>Cressa truxillensis</i>	CRTR
<i>Cuscuta salina</i>	CUSA
<i>Distichlis spicata</i>	DISP
<i>Frankenia salina</i>	FRSA
<i>Glaux maritima</i>	GLMA
<i>Grindelia stricta</i>	GRST
<i>Jaumea carnosa</i>	JACA
<i>Juncus balticus</i>	JUBA
<i>Lepidium latifolium</i>	LELA
<i>Lilaeopsis masonii</i>	LIMA
<i>Limonium californicum</i>	LICA
<i>Lotus corniculatus</i>	LOCO
<i>Plantago lanceolata</i>	PLLA
<i>Polygonum</i> sp.	POLY
<i>Potentilla anserina</i>	POAN
<i>Salicornia virginica</i>	SAVI
<i>Scirpus acutus</i>	SCAC
<i>Scirpus americanus</i>	SCAM
<i>Scirpus californicus</i>	SCCA
<i>Sonchus oleraceus</i>	SOOL
<i>Trifolium wormskioidii</i>	TRWO
<i>Triglochin maritima</i>	TRMA
<i>Typha angustifolia</i>	TYAN

Table 2. List of species encountered at Fagan Slough, 1999-2000.

Species name	Coded Name
<i>Apium graveolens</i>	APGR
<i>Atriplex triangularis</i>	ATTR
<i>Baccharis douglasii</i>	BADO
<i>Cordylanthus mollis</i>	COMO
<i>Cuscuta salina</i>	CUSA
<i>Distichlis spicata</i>	DISP
<i>Glaux maritima</i>	GLMA
<i>Grindelia stricta</i>	GRST
<i>Jaumea carnosa</i>	JACA
<i>Juncus balticus</i>	JUBA
<i>Lepidium latifolium</i>	LELA
<i>Limonium californicum</i>	LICA
<i>Polygonum</i> sp.	POLY
<i>Potentilla anserina</i>	POAN
<i>Rumex crispus</i>	RUCR
<i>Salicornia virginica</i>	SAVI
<i>Scirpus acutus</i>	SCAC
<i>Scirpus americanus</i>	SCAM
<i>Scirpus californicus</i>	SCCA
<i>Scirpus maritimus</i>	SCMA
<i>Typha angustifolia</i>	TYAN
<i>Typha latifolia</i>	TYLA

Table 3. List of species encountered at Petaluma Marsh, 1996-1997 (from Sanderson et al., 2000).

Species name	Coded Name
<i>Achillea millefolium</i>	ACFO
<i>Atriplex patula</i>	ATPA
<i>Baccharis pilularis</i>	BAPI
<i>Cuscuta salina</i>	CUSA
<i>Distichlis spicata</i>	DISP
<i>Frankenia salina</i>	FRSA
<i>Grindelia stricta</i>	GRST
<i>Jaumea carnosa</i>	JACA
<i>Lepidium latifolium</i>	LELA
<i>Rumex crispus</i>	RUCR
<i>Salicornia virginica</i>	SAVI
<i>Scirpus robustus</i>	SCRO
<i>Spartina foliosa</i>	SPFO

Table 4. Cross-sectional areas of tidal channels within study sites.

Rush Ranch

Channel System	Typical Depth (m)	Typical Width (m)	Representative Cross-section (m ²)
Sunglass Slough	1.25	3.35	4.19 (range 0.125 – 13.685)
Good-For-Nothing Slough	0.95	1.93	1.83 (range 0.075 – 21.6)

Fagan Slough

Channel System	Typical Depth (m)	Typical Width (m)	Representative Cross-section (m ²)
Fagan Slough	1.35	4.5	6.075 (range 1.5 – 9.0)
Steamboat Slough	1.45	8.0	11.6 (range 6.0 – 30.0)

Table 5. Interannual comparison (paired t-tests) of quadrat cover values for selected species at Rush Ranch (1998-1999) and Fagan Slough (1999-2000).

Hypothesized Difference = 0

Rush Ranch		Fagan Slough	
<i>Species</i>	Significance	<i>Species</i>	Significance
<i>Typha angustifolia</i>	N.S.	<i>Typha angustifolia</i>	N.S.
<i>Scirpus acutus</i>	N.S.	<i>Scirpus acutus</i>	N.S.
<i>Potentilla anserina</i>	N.S.	<i>Scirpus americanus</i>	N.S.
<i>Scirpus americanus</i>	p<0.0001	<i>Lepidium latifolium</i>	N.S.
<i>Lepidium latifolium</i>	p=0.0004	<i>Juncus balticus</i>	N.S.
<i>Juncus balticus</i>	N.S.	<i>Salicornia virginica</i>	N.S.
<i>Scirpus californicus</i>	N.S.	<i>Jaumea carnosa</i>	N.S.
<i>Apium graveolens</i>	N.S.	<i>Distichlis spicata</i>	N.S.
<i>Salicornia virginica</i>	N.S.	<i>Grindelia stricta</i>	N.S.
<i>Jaumea carnosa</i>	N.S.		
<i>Distichlis spicata</i>	N.S.		
<i>Frankenia salina</i>	p<0.0001		

Table 6. Regression analysis for Rush Ranch species versus local elevation or distance from tidal slough.

<u>Species</u>	<u>Elevation Adjusted r²</u>	<u>Distance Adjusted r²</u>
TYAN	0.049	0.062
SCAC	0.006	0.030
SCAM	0.047	0.243
JUBA	0.004	0.478
SCCA	0.007	0.029
GLMA	0.009	0.111
TRMA	0.032	0.225
SAVI	0.007	0.185
JACA	0.003	0.195
DISP	0.028	0.403
GRST	0.018	0.004
mean	0.019	0.179

Table 7. Regression analysis for Fagan Slough species versus local elevation or distance from tidal slough.

<u>Species</u>	<u>Elevation Adjusted r²</u>	<u>Distance Adjusted r²</u>
SCAC	0.124	0.006
SCAM	0.111	0.023
LELA	0.018	0.147
JUBA	0.234	0.007
SAVI	0.048	0.205
DISP	0.172	0.028
CUSA	0.067	0.102
SCMA	0.121	0.032
mean	0.112	0.069

Table 8. D_{75} criteria for selected species in three tidal marshes.

Tidal Marsh Location			
	Rush Ranch	Fagan Slough	Tule Slough
Streamside Zone	<i>Scirpus americanus</i> $D_{75} = 25.0$	<i>Scirpus americanus</i> $D_{75} = 15.0$	<i>Spartina foliosa</i> $D_{75} = 1.5$
Transition Zone	<i>Juncus balticus</i> $D_{75} = 60.0$	<i>Juncus balticus</i> $D_{75} = 20.0$	<i>Frankenia salina</i> $D_{75} = 6.0$
Marsh Plain	<i>Salicornia virginica</i> $D_{75} = 70.0$	<i>Salicornia virginica</i> $D_{75} = 30.0$	<i>Salicornia virginica</i> $D_{75} = 14.0$



Figure 4. Map of Tule Slough Area/Petaluma Marsh, Sonoma County, CA, USA.

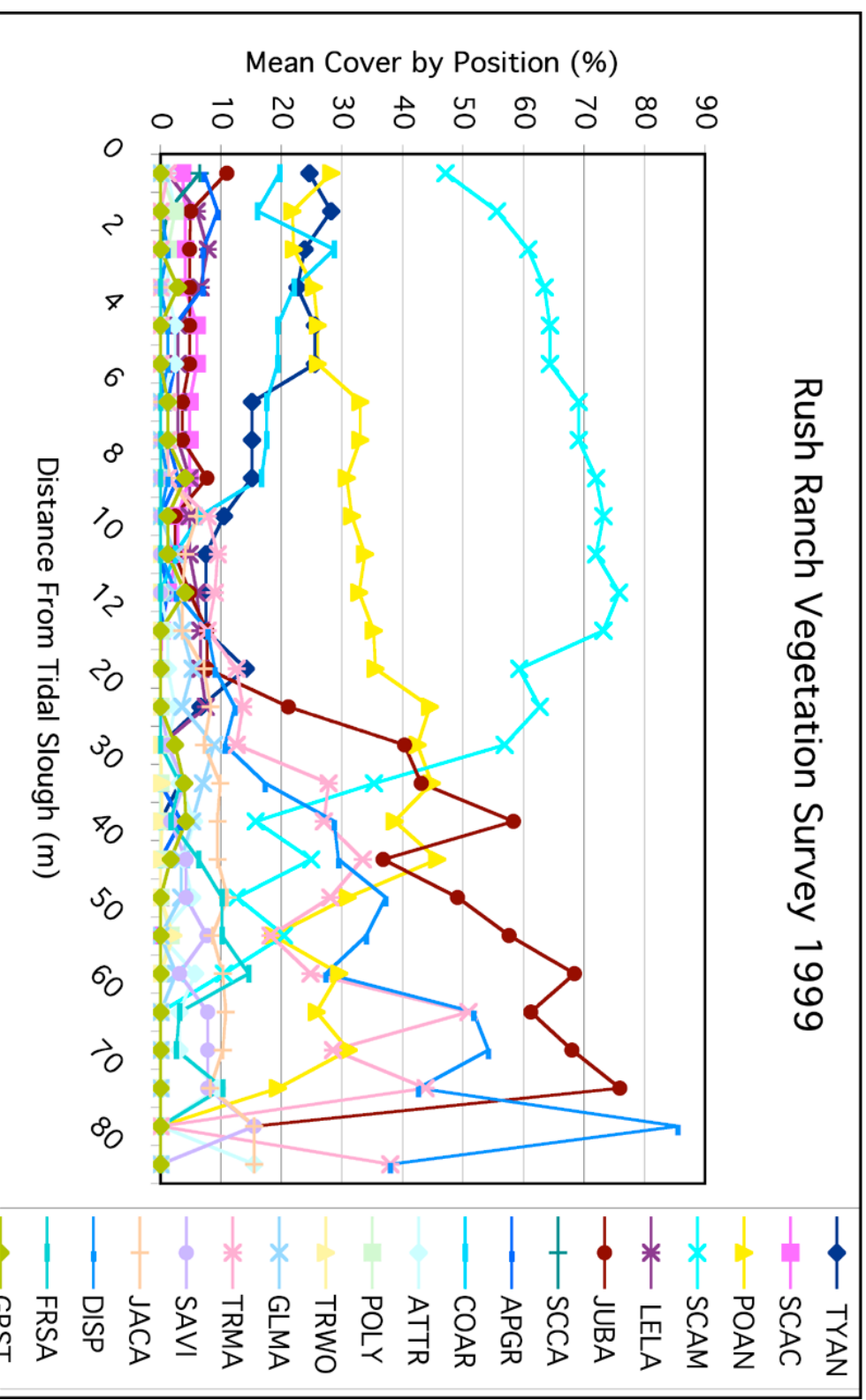


Figure 7. Vegetation Survey showing species' mean cover value by position at Rush Ranch.

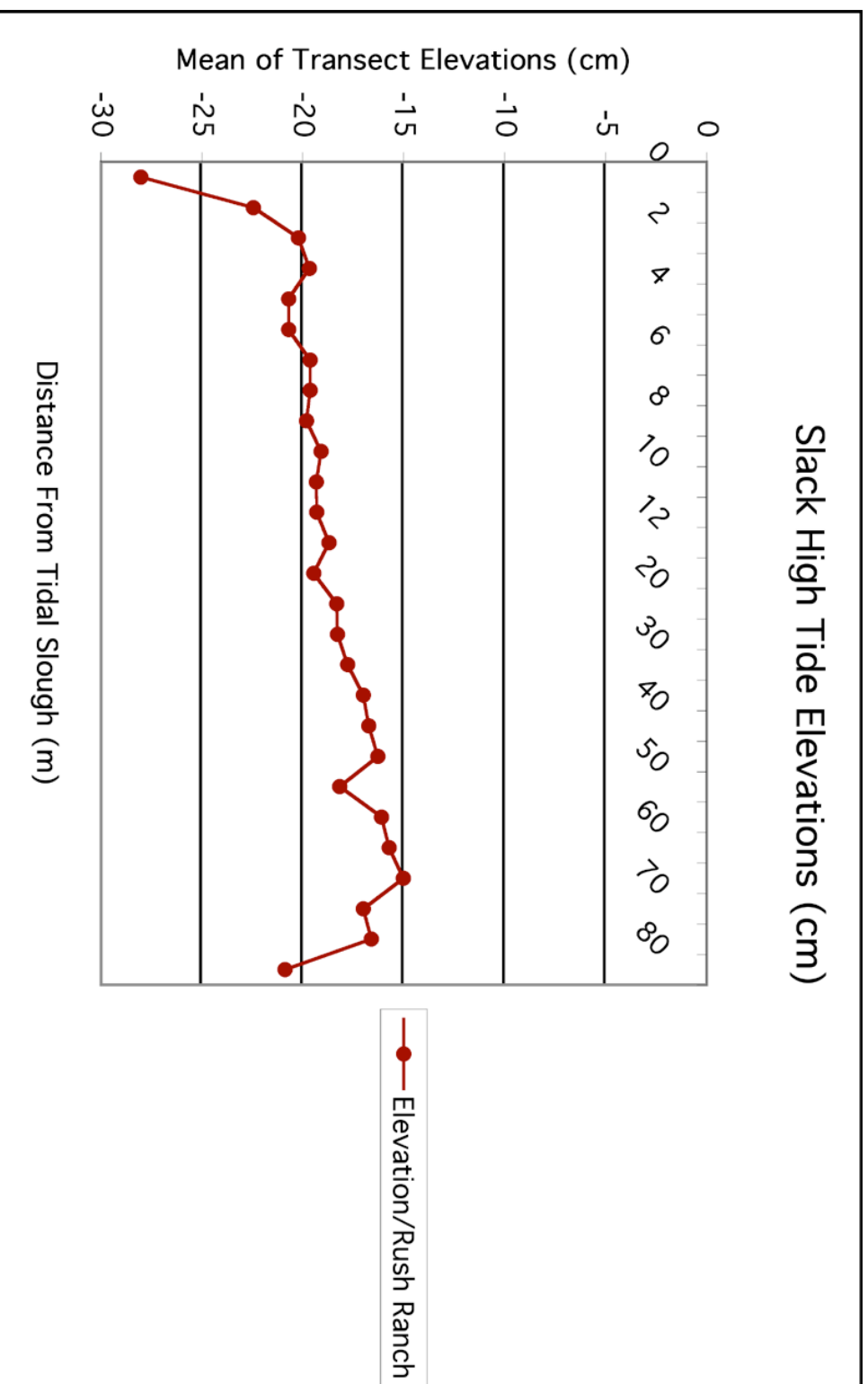


Figure 8. Mean elevations by transect location at Rush Ranch.

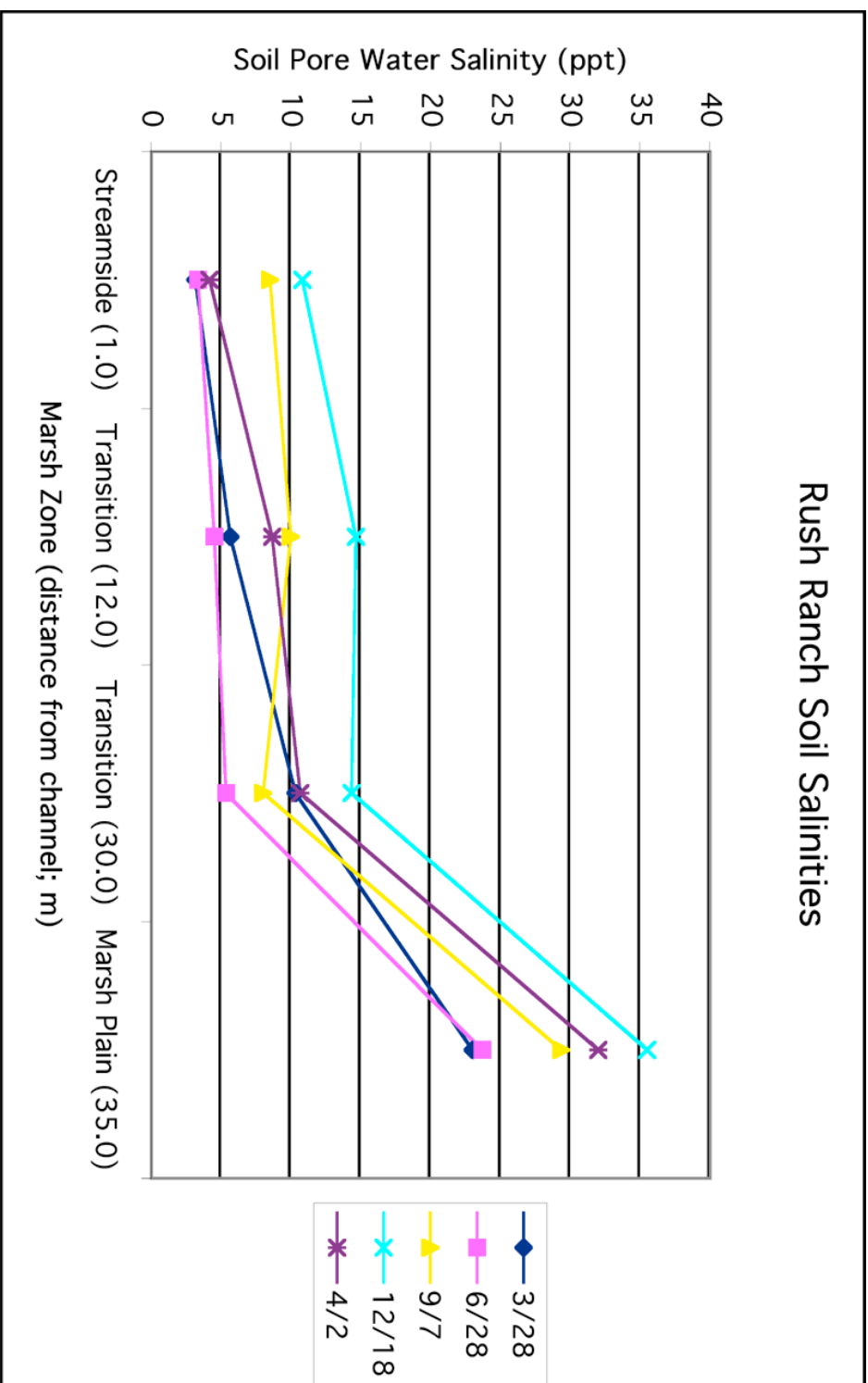


Figure 11. Quarterly soil pore water salinities, Rush Ranch, 2000-01.

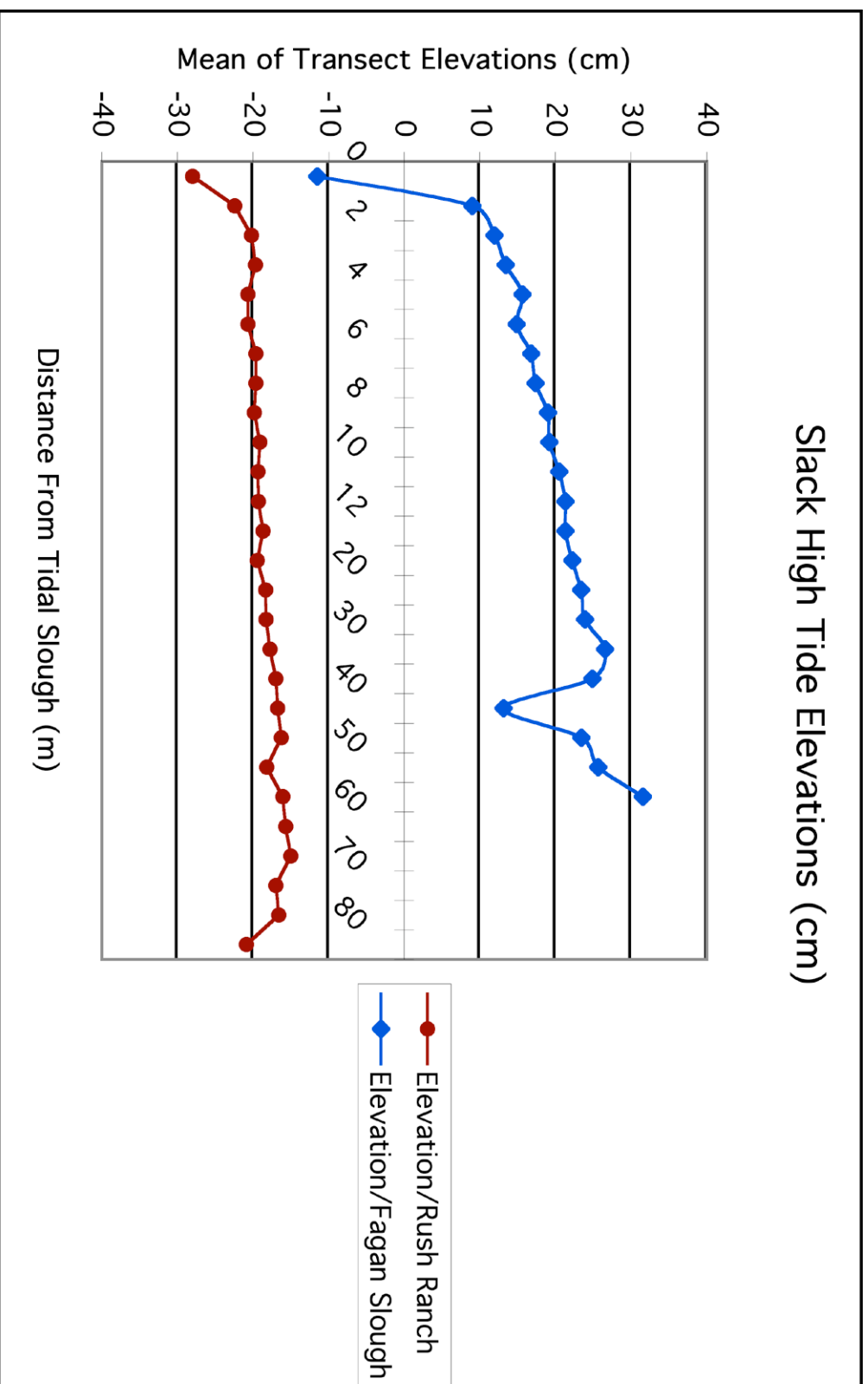


Figure 12. Average elevation profiles for vegetation transects at Rush Ranch and Fagan Slough (calibrated using slack high tide).

Fagan Slough Vegetation Survey 1999

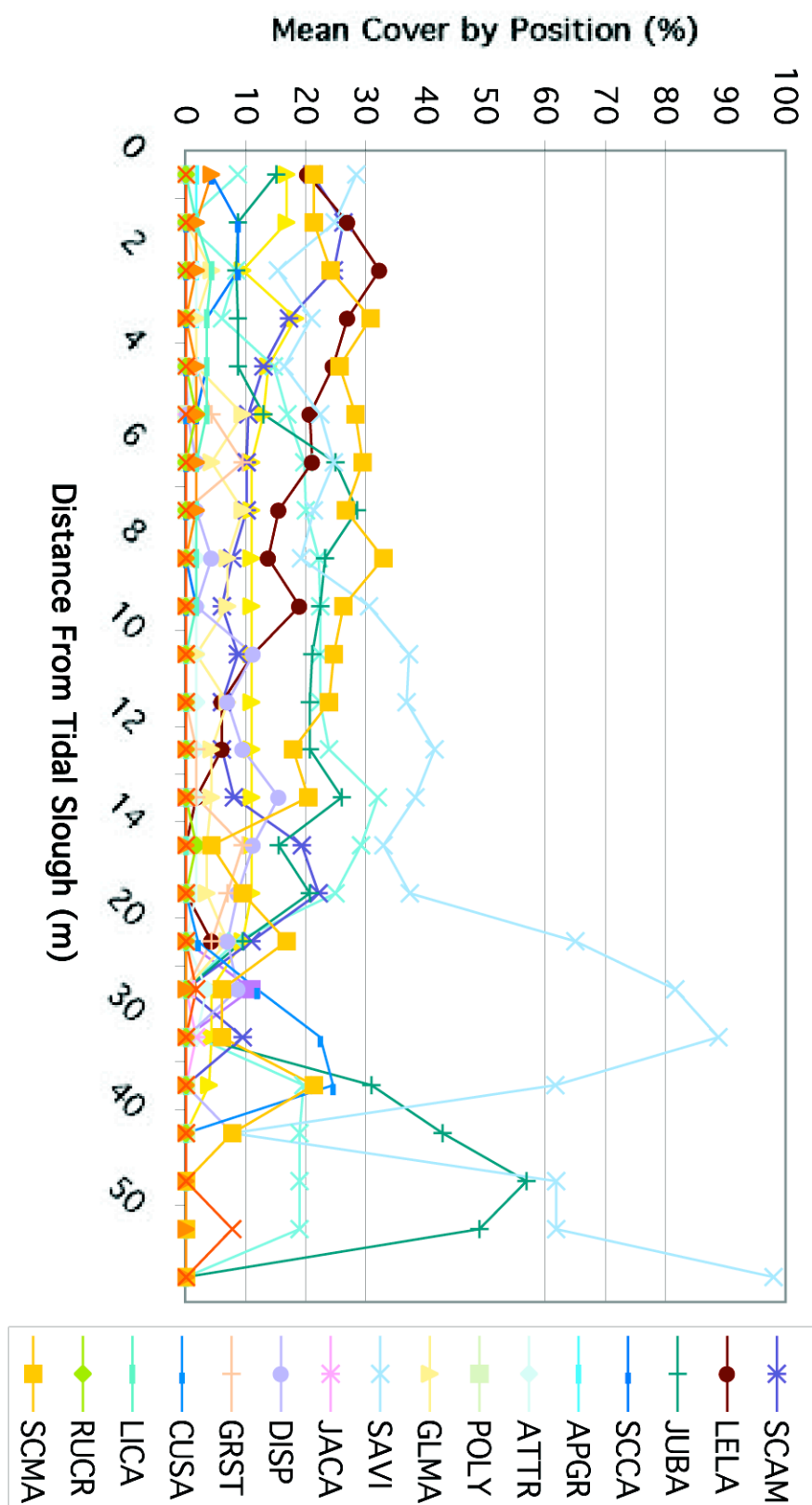


Figure 17. Vegetation survey showing species' mean cover value by position at Fagan Slough.

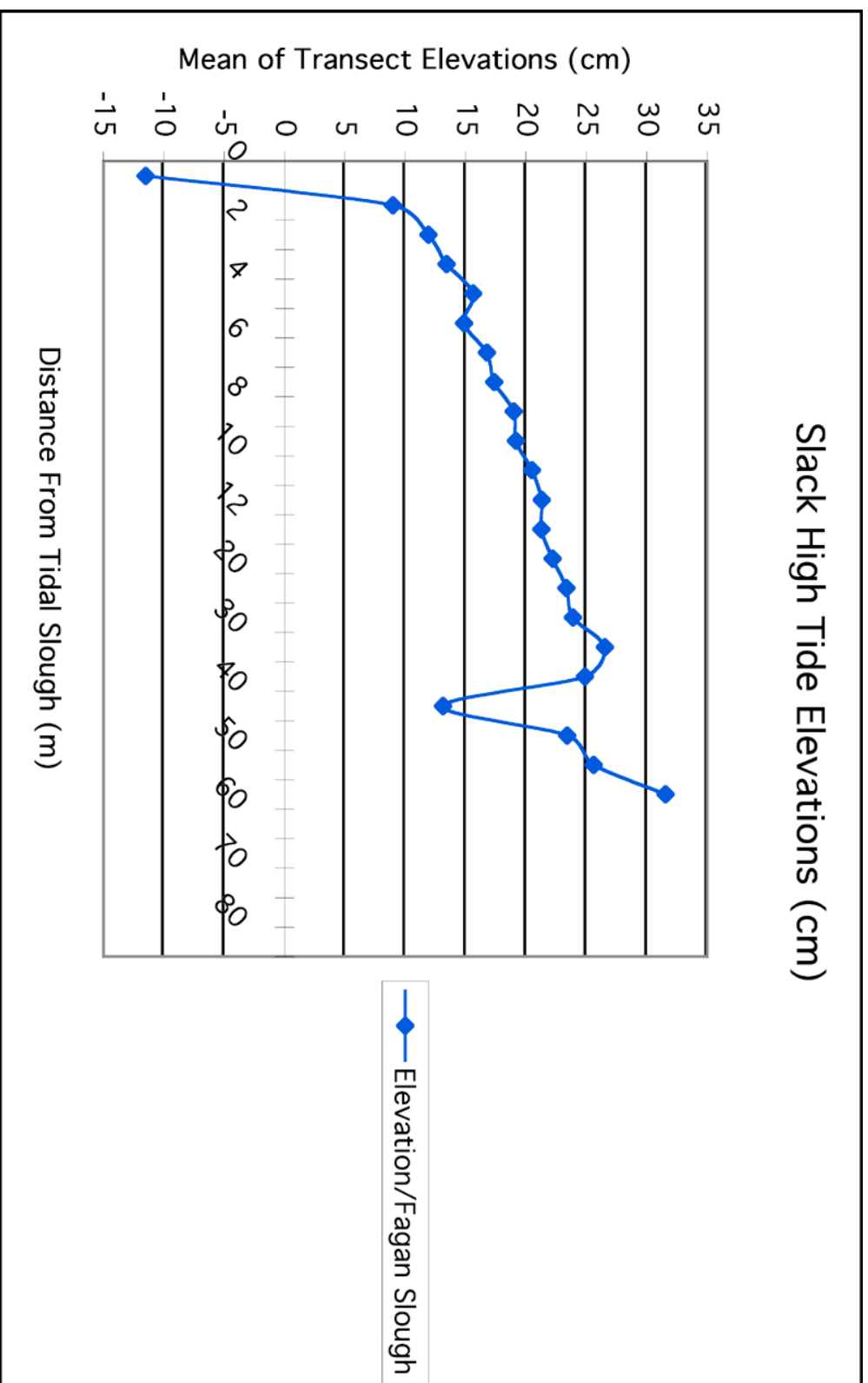


Figure 18. Mean elevations by transect location at Fagan Slough.

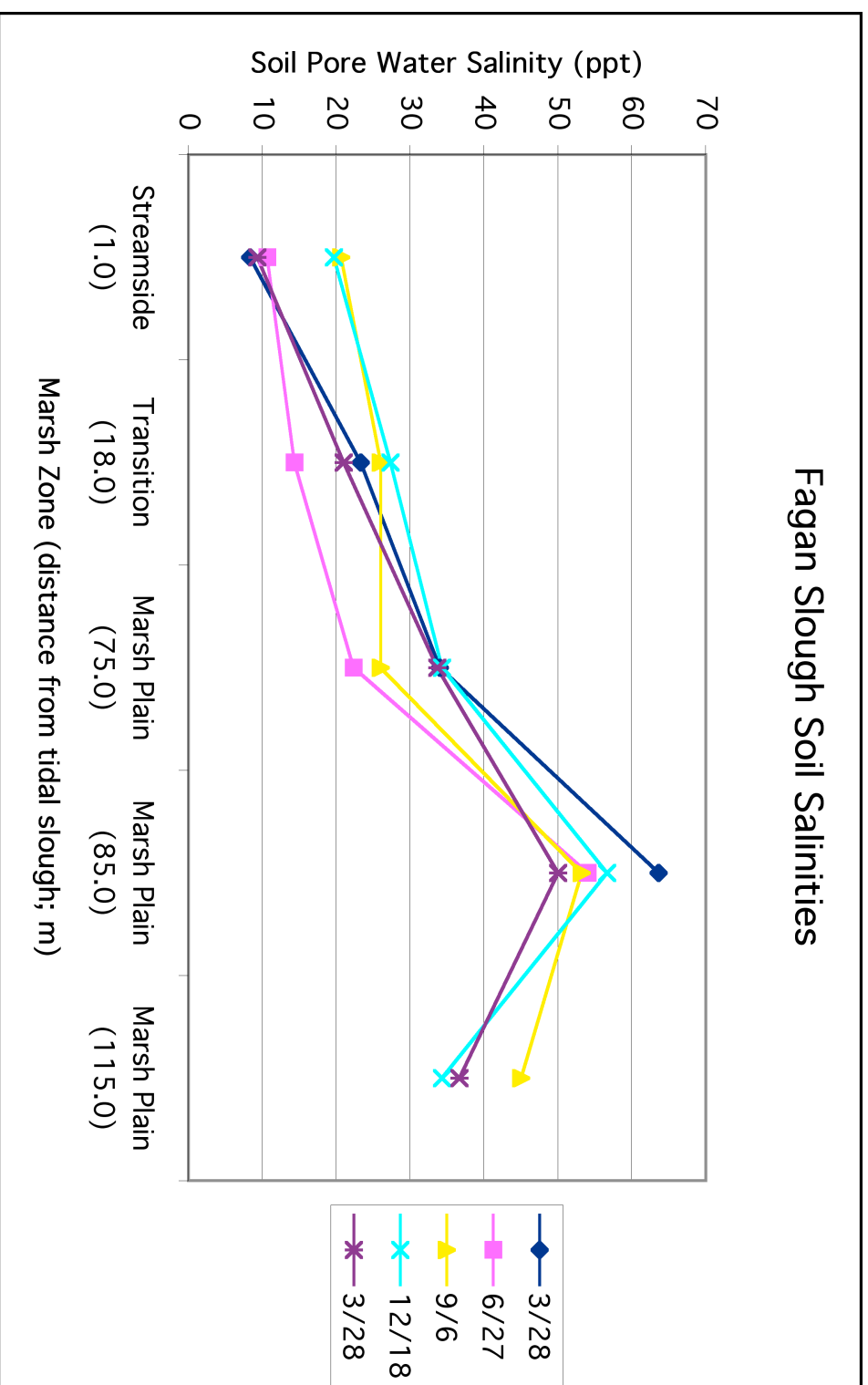


Figure 19. Quarterly soil pore water salinities, Fagan Slough, 2000-01.

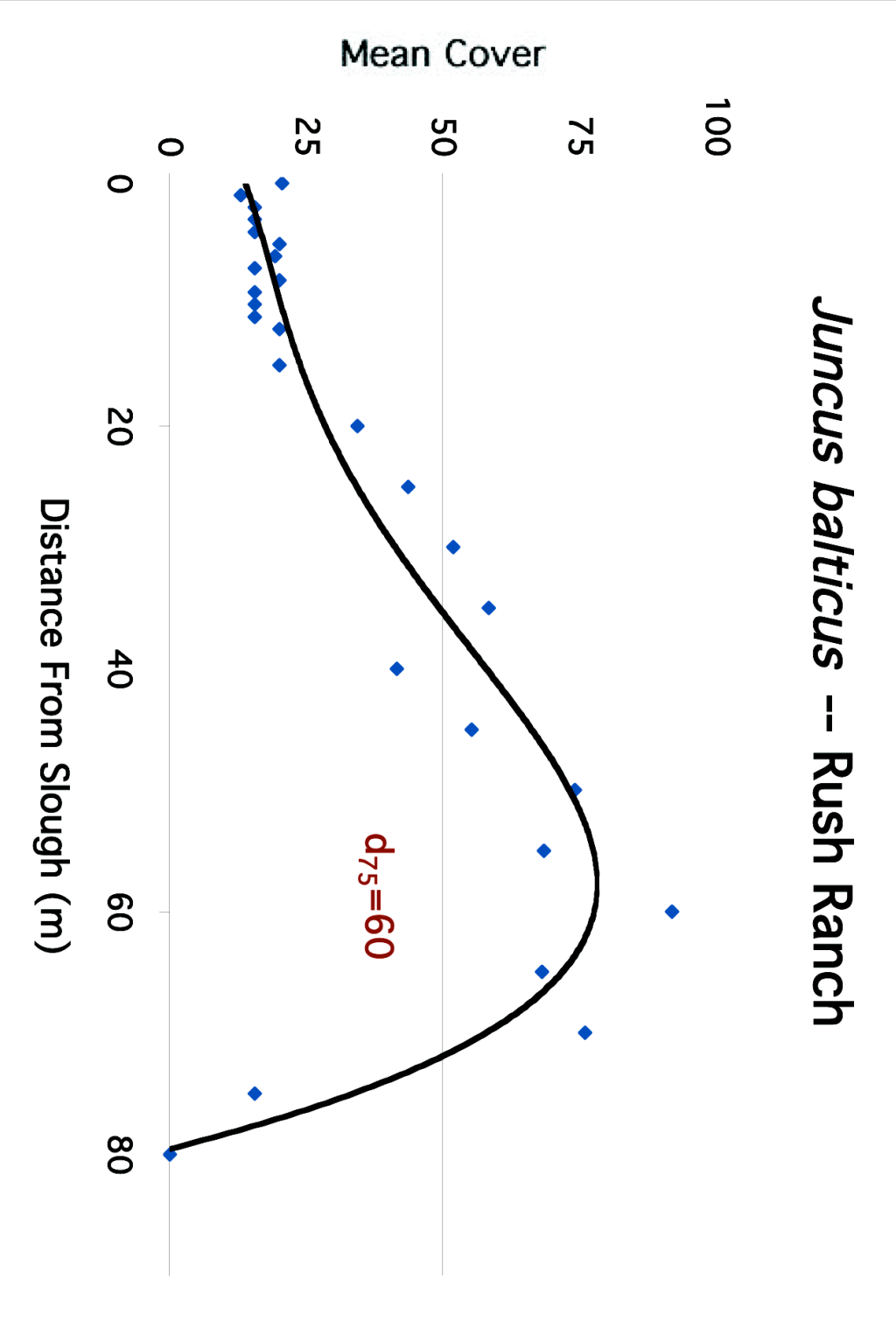


Figure 21. D_{75} criterion for *Juncus balticus* at Rush Ranch.

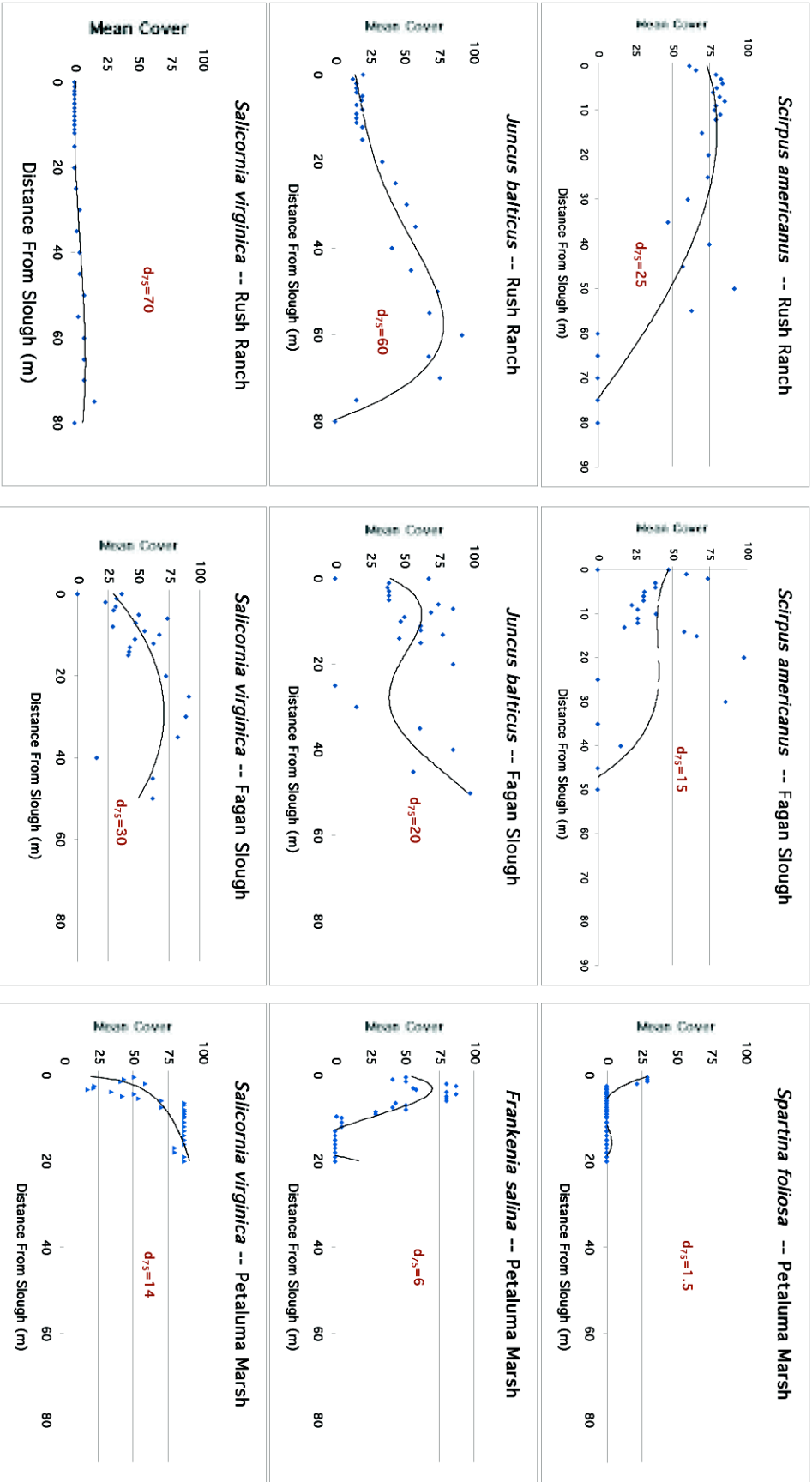


Figure 22. Data and D_{75} criteria from three tidal marshes in the San Francisco Bay/Delta Estuary, CA. Plot lines added to aid visualization.

Experimental Verification of Soil Salinity as the Dominant Control of Vegetation Productivity in Tidal Marshes of the San Francisco Bay Estuary

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Abstract

Vegetation patterns in tidal marsh ecosystems within the San Francisco Bay/Delta are determined partly through the interaction of tidal hydrology and regional salinity. In this study, several species of tidal marsh plants (*Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica*) were subjected to various field regimes of moisture and salinity typical of regional tidal marshes in order to measure their productivity response. Laboratory manipulations of *Distichlis spicata* within moisture and salinity treatments show differences in productivity attributable to one both factors. Experimental exposure of plants to natural and laboratory soil and hydrologic conditions provides evidence for physical control of the existing tidal marsh vegetation pattern, particularly where soil salinity gradients are found.

Introduction

Recent efforts to establish regional monitoring programs for wetlands resources of the San Francisco Bay/Sacramento-San Joaquin Delta Estuary (Bay/Delta Estuary) have revealed that at least two physical parameters are needed in any appropriate framework for guiding regional wetlands protection and restoration: hydrology and salinity (Collins, 2001; Collins et al., 2001). The physiographic and geomorphic framework of the Bay/Delta Estuary provide strong hydrologic and salinity gradients upon which wetland protection and restoration efforts may be based (Mahall and Park, 1976a; Mahall and Park, 1976b; Mahall and Park, 1976c; Ustin et al., 1982; Nichols et al., 1986; Cheng et al., 1993; Dedrick, 1993; Dedrick and Chu, 1993; Keldsen and Farmer, 1993; Wells, 1995; Ingram et al., 1996; Goman and Wells, 2000), and wetlands landscape units have been shown to show strong relationships of vegetation to local patterns of hydrology and salinity (Percy et al., 1982; Pezeshki et al., 1987; Callaway et al., 1990; Kenkel et al., 1991; Shipley et al., 1991; Bertness et al., 1992; Wilson et al., 1996; Ungar, 1998; Howard and Mendelssohn, 1999; Howard and Mendelssohn, 2000; Sanderson, et al., 2000; Greiner La Peyre et al., 2001; Sanderson et al., 2001; Culberson et al., in review). This paper presents experiments that examine productivity responses from several wetland species (*Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica*) that dominate wetland landscapes within the Bay/Delta Estuary (Siegel, 1993;

Culberson et al., 2000; Foin et al., 2000). Recent research has shown that vegetation zonation in the Estuary is related to location of tidal channels (Sanderson et al., 2001; Sanderson et al., 2000; Culberson et al., in review). The location of tidal channels contributes to the establishment of soil pore water salinity gradients in marshes of the Estuary (Balling and Resh, 1982; Collins, 2001; Culberson et al., in review), and soil salinity is thought to be an important determinant of plant productivity in brackish to euryhaline marshes.

Materials and Methods

Species and plant collection/placement

The four species selected for this study are found as local dominants in at least two of three widely-separated marshes within the San Francisco Bay/Delta Estuary (Culberson et al., in review). *Scirpus americanus* is a streamside dominant at Rush Ranch in the Suisun Marsh complex (38°12'30" N, 122°2'30" W) in Solano County, CA, and at Fagan Slough near the Napa River (38°13'28" N, 122°17'30" W), Napa County, CA. *Juncus balticus* is a transition-zone dominant species found at Rush Ranch and Fagan Slough. *Distichlis spicata* is a transition zone species at Fagan Slough and at the Petaluma Marsh adjacent to the Petaluma River (38°12'20" N, 122°32'32" W) in Sonoma County, CA, and a marsh plain dominant at Rush Ranch. *Salicornia virginica* is a marsh plain dominant at Petaluma Marsh and at Fagan Slough (Figure 1).

Plant material was collected from the field or obtained locally from restoration nurseries in the fall of 1999, propagated and over-wintered under freshwater conditions in Davis, CA, and transplanted with minimal rooted soil into the field in April 2000. Individual propagated plants were selected for uniform size and growth habit for planting. Harvest of the field transplants occurred in September 2000. Mesocosms were planted in June 2000 with *Distichlis spicata* and harvested in November 2000. Field transplants were made by placing each plant into an excavated hole large enough to accommodate a 0.6-gallon perforated root bag and filling the bag by replacing the native topsoil around the plant. Mesocosms were 18-gallon plastic containers filled to a depth of 30 cm with soil into which plants were placed.

Experimental Design – Field Transplants

Field transplants were used to assess productivity responses in each of the four plant species in three marsh zones: streamside, transition, and marsh plain areas. 20 replicate plants of each of the four species were placed into each zone of the marsh in a reciprocal transplant design at Fagan Slough and Rush Ranch, where salinity in the incoming tidal water averages 15 and 2 parts per thousand (ppt), respectively. At Fagan Slough, an additional set of 20 plants was divided equally between two additional marsh plain zones noted for their high salinity or robust *Salicornia virginica* growth habit (referred to as “Marsh Plain (85.0)” and “Marsh Plain (115.0)” zones). Plants were located randomly with respect to position along a 60 m transect placed parallel to the nearest tidal channel, spaced at 0.75m intervals.

Soil pore water salinities were obtained by sampling water collected in stilling wells perforated at a depth of 15 cm below the soil surface and reading total salinity on a hand-held, temperature-compensated salinity refractometer (Sper Scientific). Reported values are means from three wells installed at each sampled location. Wells were installed near the midpoint of each transplant transect, and covered with caps to prevent overmarsh tides from contaminating samples.

Experimental Design – Mesocosm Experiment

Mesocosm environments were utilized to provide precise control over hydrologic and salinity treatments to tidal marsh plant species. Productivity response to combinations of salt and water availability similar to those found under natural marsh field conditions were sought to assess the relative importance of each to zone-based tidal marsh productivity. Commercially available (Rubbermaid®) 18-gallon plastic storage containers were arranged in ranks on greenhouse benches and plumbed to receive variable water supply (daily versus every fourth day watering) and salinity (0 versus 15 ppt). Drains were installed that permitted upper water storage level coincident with the soil surface level (30 cm depth) or coincident with 0.5 soil surface level (15 cm depth). Treatments were blocked into “salt” versus “no salt” groups, and randomly assigned within blocks for water supply and drainage depth. Four individual propagations of *Distichlis spicata* or *Salicornia virginica* were installed into each container, placing one plant into each soil surface quadrant. Water supply was monitored weekly for salinity, and adjusted as necessary to 15 ppt using additions of water and/or commercially

available marine sea salt mixture. Treatments were maintained for the duration of the experiment, following a one-week hardening period during which salinity was gradually increased to 15 ppt within the “salt” treatment block. No plant mortalities or significant shocks to transplants were noted within the first month of treatment.

Harvest and Processing

All plants were harvested whole (except for every fourth plant in the mesocosm study, in which roots were harvested by dividing the soil column containing roots into two equal horizons, “upper roots” and “lower roots”), washed of soil, and dried at 60°C for one week. Above and belowground portions of each plant were determined for weighing. Mass was determined to ± 0.01 g.

Data Analysis

Total dry weights and partitioned dry weights (shoots, roots, upper roots, lower roots) were examined as a method of assessing plant biomass productivity under different treatment conditions. ANOVA analysis using StatView 5.01 (SAS Institute Inc., 1998) was used to characterize treatment effects. Means for each treatment are used as a basis for comparison between species (N=20 for reciprocal transplants, N=12 for mesocosm treatments).

Results

Reciprocal Transplants—Fagan Slough

Average salinity for water entering the marsh via the Napa River/Fagan Slough was 15 ppt. Streamside zones have soil salinities similar to incoming tidal water salinities, but soil salt concentrations increase with distance onto the marsh plain. Soil salinities within the rooting zone at Fagan Slough increase with distance from the tidal slough, up to the “Marsh Plain (115.0)” position which is influenced by a slough near the upland edge of the marsh (Figure 2). Within the marsh plain itself differences are found, with high salinities (50 ppt or more) encountered furthest from apparent channels, peaking at the Marsh Plain (85.0) location. These high salinity marsh plain locations are covered by a near monoculture of *Salicornia virginica*, with patchy infestations of *Cuscuta salina*, a hemiparasite, and occasionally *Juncus balticus* and *Distichlis spicata* (Table 1). Early growing season salinities (3/2000 and 3/2001) show larger increases in

soil salinities when moving from streamside (10 ppt) to transition (20 ppt) to marsh plain zones (33 ppt) than during later periods, and are assumed important to the determination of vegetation productivity. This salinity gradient persists throughout the year (with limited variability) and shows an overall increase in value as rainfall ceases during the summer and fall.

Transplants were expected to respond to the salinity gradients described by displaying decreasing productivity as salinity increases. This effect should be more pronounced in streamside species than in marsh plain species due to their higher sensitivity to soil salinity. Dry weight biomass means for *Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica* for each of the described transplant zones are shown in Figure 3. ANOVA results indicate that species, zone, and species by zone differences are present (Table 2). For the most salt-sensitive species, *Scirpus americanus*, the transplants behaved as expected, showing lowered productivity under increasing levels of soil salinity. Less salt-sensitive species showed more limited responses to increasing soil salinities (particularly *Juncus balticus* and *Salicornia virginica*). When all species are considered together, a consistent pattern of lowered productivity is found where soil salinities are higher, as found throughout the marsh plain zone (Figure 4). An exception to this pattern is within the streamside zone, where biological interactions (primarily light competition) diminished transplant performance (see below).

Individual species' responses vary as a result of their individual characters of sensitivity to salt, growth habit, and tolerance of shading: ***Scirpus americanus***: Except within the streamside zone, biomass accumulation is inversely related to soil salinity found within the transplant zones, a productivity response profile consistent with salt-stress limitation. This productivity trend by zone is present within vegetation surveys of *Scirpus americanus* at Fagan Slough (Culberson et al., in review), which indicate higher productivity and cover values under lower soil salinity conditions. These results have also been reproduced in recent mesocosm studies (R.O. Spent, personal communication). ***Juncus balticus***: There are no differences between zones for this species. Of note is the tolerance shown by *Juncus balticus* across the range of salinities encountered while maintaining productivity. *Juncus balticus* is not widely dominant in

the landscape at Fagan Slough, but can be found at moderate cover values throughout the marsh. It is prominent at the transition between streamside and marsh plain vegetation, where taller *Scirpus* species are gradually replaced by the highly salt-tolerant *Salicornia virginica* (Culberson et al., in review). Demonstrated productivity at lower cover values across a range of soil salinities is characteristic for this species (Culberson et al., in review; Foin et al., 2000), though under conditions of mild soil salinity *Juncus balticus* is locally dominant (Culberson et al., in review). ***Distichlis spicata*:** Biomass production within the “Transition” and “Marsh Plain (85.0)” zone treatments are higher than within other zones for this species. This result is puzzling even when the influence of competition for light resources is included, since it does not account for reduced productivity found at the “Marsh Plain (75.0)” location, where no such competition is noted – the dominant extant species at this location is *Salicornia virginica* (Table 1). The results from *Distichlis spicata* do not correspond with documented patterns of soil salinity detailed here. Other species that show evidence of salinity tolerance (*Juncus balticus* and *Salicornia virginica*) also have slightly higher mean biomass production at the “Marsh Plain (85.0)” location than in other zones, leading to questions of whether some undocumented resource availability at this site may have an influence. Further information detailing the nature and character of groundwater resources at this site relative to others at Fagan Slough are needed to resolve this issue, but are beyond the scope of the present study. ***Salicornia virginica*:** This species exhibited consistent productivity across the known salinity gradient, with no decrease in biomass production as the result of increases in soil salinities. Lack of significant reduction in biomass production under high soil salinity is expected for this species, known for its ability to persist in salt marsh environments considered too dry or too saline for other species. *Salicornia virginica* dominates the marsh plain environment at Fagan Slough (Culberson et al., in review), and the species is found throughout the marsh (Table 1).

Reciprocal Transplants – Rush Ranch

Soil salinities within transplant sites at Rush Ranch show little increase with increasing distance from the tidal slough, although they generally rise over the course of the year (Figure 5). Nonetheless, differences in soil salinity and plant productivity within transplant experiments at Rush Ranch and Fagan Slough are noted (see also Foin et al.,

2000; Culberson et al., in review). Dry weight biomass means for *Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica* within the described transplant zones show patterns of increasing biomass with distance from tidal channel (Figure 6). ANOVA results indicate that species, zone, and species by zone differences are present (Table 3). These patterns exist in the absence of any significant salinity gradient. They are the inverse of existing patterns of biomass and mean canopy height among the natural vegetation at Rush Ranch (Foin et al., 2000; R.O. Spenst, personal communication), and are consistent with a decrease in competition for light as distance from channel increases (Figure 7). The presence of this productivity pattern within transplants is in sharp contrast with the pattern at Fagan Slough, where an evident streamside to marsh plain salinity gradient exists and soil salinities are 2-4 times higher. Fagan Slough transplants respond to conditions of higher soil salinity through decreases in biomass accumulation as distance from channel increases, whereas transplant biomass accumulation within our study site at Rush Ranch, an area largely devoid of salt-stress effects, increases with distance from channel as the result of response to biological influences (competition).

Transplants show an overall pattern of lowered biomass accumulation at Rush Ranch under conditions of reduced salinity stress (versus Fagan Slough) because biological factors (competition for light resources) are more dominant in the more freshwater landscape (Table 4). Biomass accumulation in transplants *within* Rush Ranch is also biologically mediated, showing an inverse relationship to existing plant biomass (Foin et al., 2000; S.D. Culberson, personal observation; R.O. Spenst, personal communication) and reduction in transplant productivity due to shading by existing vegetation. Considered individually without regard to marsh zone, species showed varied responses to the different environmental conditions at each marsh (Table 4). Mean difference as “Total for all species” indicates that biomass production for the suite of transplanted species was lower at Rush Ranch due to across-species shading effects. No differences in either *Scirpus americanus* or *Distichlis spicata* were noted between marshes – these species are normally more productive under fresher conditions, but do not grow as well under limited light. *Juncus balticus* grew better on the whole at Rush Ranch under fresher conditions, and did not show as much sensitivity to light as to

increased salinity at Fagan Slough. *Salicornia virginica* demonstrated tolerance to higher salinities at Rush Ranch, and/or sensitivity to low light levels and produced significantly more biomass at Fagan Slough than at transplant sites in Rush Ranch.

Mesocosm Treatments – Distichlis spicata

Dry weight biomass means for *Distichlis spicata* under the range of experimental treatments examined in the mesocosm portion of this study show expected responses to various quantities of available water and dissolved salts (Figure 8). There is a general trend of decreasing biomass production with a decrease in water supply (decreasing flooding from daily to every fourth day -- termed “weekly” hereafter -- and increasing depth of drainage from 0 to 15 cm below the soil surface). The effect of decreased water on productivity is seen in treatments with and without added salt. Decreasing the frequency of watering (from daily to weekly) lowers productivity by 16.5% across all plants receiving this treatment. Lowering the level of the drains within the mesocosms by 15 cm results in a decrease in productivity of 21.0%. Treatment effects are significant between all quantities of available water in the salted mesocosms ($p < 0.030$). Treatment effects in the unsalted mesocosms are also significant ($p < 0.03$) in reducing plant productivity for all comparisons when not comparing adjacent bars (e.g. when reading from left to right, bar #1 represents mean differences from bars #3 and #4 but not #2, and so on).

Likewise, there is a general decrease in overall *Distichlis spicata* productivity across all water treatments when salt is added. Those plants receiving 15 ppt total salinity in input water produced 26.5% less biomass on average than those plants receiving no salinity ($p < 0.0001$). This percentage decrease in productivity under the presence of salt means the overall reduction in biomass accumulation for *Distichlis spicata* was larger due to salt than due to reduced quantities of available water (either through reduced frequency of flooding or through lowered water table).

These results support our view that soil pore water salinity and water availability are important factors structuring vegetation zonation across the marsh landscape by directly affecting plant productivity. The effect of salt is found to be greater than the effect of reduced water availability (Table 5). While observations reported in this study are limited to *Distichlis spicata*, these effects are also found in current mesocosm

experiments involving *Scirpus acutus*, *Scirpus americanus*, and *Lepidium latifolium* (Spent and Foin, unpublished data).

It is interesting to note in the high light environment provided by the mesocosm study (no inter-specific shading), *Distichlis spicata* biomass accumulation was 10 –30 times that found within the Fagan Slough and Rush Ranch transplant portion of this study, with otherwise similar soil moisture and salinity conditions. This provides supporting evidence that light limitation was indeed important to *Distichlis spicata* biomass productivity within the transplant environment.

Discussion

Results from these field transplant and mesocosm experiments support our conceptual model of vegetation zonation in tidal marsh ecosystems (Foin et al., 2000; Sanderson et al., 2000; Sanderson et al., 2001; Culberson et al., in review), in that (1) location of the tidal channel network supplying water to the marsh landscape is strongly related to vegetation productivity through regulation of available moisture and soil salinity, and (2) regional patterns of tidal salinity are related (through regulation of soil salinity and plant species productivity) to the resulting vegetation zonation found on a local level. We demonstrate that soil salinity is more important than water availability for regulating short-term plant productivity in marsh plant species regularly experiencing tidal inputs. By regulating short-term plant productivity we assert longer-term control by soil salinity over regional vegetation zonation in the studied marshes (Culberson et al., in review). These regulatory effects are demonstrated in the field at Rush Ranch and Fagan Slough and in laboratory mesocosms for four species of plants commonly dominating different marsh zones of the San Francisco Bay/Delta Estuary: *Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica*.

Vegetation productivity on the marsh landscape depends upon the availability of water supplied to the marsh via tidal channels and the accumulation of salts through subsequent evapotranspiration. The resulting gradients of moisture and salinity result in characteristic zonation patterns documented within the Estuary (Foin et al., 2000; Sanderson et al., 2000; Sanderson et al., 2001; Culberson et al., in review). Moving downstream within the Bay/Delta corresponds to an increase in salinity, and to a decrease

in the width of the streamside, channel-influenced, zone of lowered accumulated salts. The transition zone also moves closer to the channels in response to increasing soil salinities inland, and the marsh plain of halophytic species expands. In the presence of sufficient available soil moisture, soil salinity becomes increasingly important to the structure of marsh vegetation as the Bay is approached.

Isolating the influence of salinity via field transplants and mesocosm studies shows we can duplicate the patterns found in tidal marshes of the Bay/Delta using physical factors to affect plant productivity. Streamside zone species (*Scirpus americanus*) show high productivity under conditions of lowered salinity and abundant water normally found associated with areas near tidal channels, but perform progressively worse as salinity increases. Transition zone species (*Juncus balticus*, *Distichlis spicata*) show wider tolerance for a range of soil salinity without suffering large decreases in productivity. Marsh plain species (*Salicornia virginica*) can survive high salinities while maintaining biomass accumulation rates, but are relatively lower in productivity overall.

We admit, however, the importance of biological factors (particularly light competition) in influencing vegetation zonation, the effects of which were previously under-appreciated within the San Francisco Bay/Delta Estuary (see, as further example, Grewell, 2000). The role of light competition is more important under benign physical conditions (lower soil salinity, higher water availability) found when moving headward (upstream) within the Estuary, or in streamside zones. This effect was particularly apparent for streamside zones at Fagan Slough and more generally at Rush Ranch for the transplant experiments presented here. Light competition may also play a role in the ‘invasibility’ of streamside zones by exotic species, such as *Lepidium latifolium*, and is currently under investigation (T.C. Foin and R.O. Spent, personal communication). These results are consistent with previous research describing biological control of vegetation pattern under physically benign conditions in other regions of North America (Pennings and Callaway, 1992; Hacker and Bertness, 1999; Bertness and Pennings, 2000; Mendelsohn and Morris, 2000).

Lastly, we draw attention to the need for adequate understanding of the relationship between the tidal channel network and ground water movement in near-surface areas of marshes within the San Francisco Bay/Delta Estuary. Preliminary data

characterizing groundwater elevation in the absence of substantial overmarsh flooding within higher marshes of the Bay Delta (particularly Petaluma Marsh and Fagan Slough) suggests soil pore water salinity may be related to water movement within the soil column, independent from channel-based tidal incursion (Collins, J.N., unpublished data; Figure 9). Notable in the water elevations at Fagan Slough (Figure 9) is that water at the “Marsh Plain (85.0)” location was always closer to the surface than at the “Marsh Plain (115.0)” location during sampling events, at times by as much as 20 cm. Examination of results from the transplant portion of this study (Figure 3) reveals that three transplanted species (*Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica*) show slightly higher biomass accumulation totals at “Marsh Plain (85.0)” than at “Marsh Plain 115.0.” We suspect these plants are responding to local water and/or salinity gradients that are only indirectly related to tidal channel influence. These gradients could be associated with linear distance from nearby tidal channels (Culberson et al., in review), with non-linear distance (Sanderson et al., 2000), or have a completely unknown relationship with local ground water movement and near-surface soil moisture availability. These gradients may change depending upon the rate of moisture removal from the ground surface through evapotranspiration, which itself may be a function of the overlying vegetation (Grewell, 2000). Whatever the relationship, more detailed study of groundwater elevation and movement, including continuous monitoring in relation to local tides, is essential to understanding resulting soil salinity. Groundwater movement may provide for vegetation an important source of relief from salt stress to plants in the absence of overmarsh tidal flooding, and more completely explain tidal marsh plant productivity and vegetation zonation.

Acknowledgements

The authors would like to thank the U.S. Fish and Wildlife Service, the California Department of Fish and Game, and the Solano County Farmlands and Open Space Foundation for permission and access to study sites described in this paper. This paper is funded by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA66RG0477, project number R/CZ-154 through the California Sea Grant College

System, and in part by the California State Resources Agency. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies. The U.S. Government is authorized to reproduce and distribute for governmental purposes. Special thanks to Mary Pakenham-Walsh, Renee Spent, and Lissa Veilleux for field assistance and laboratory support.

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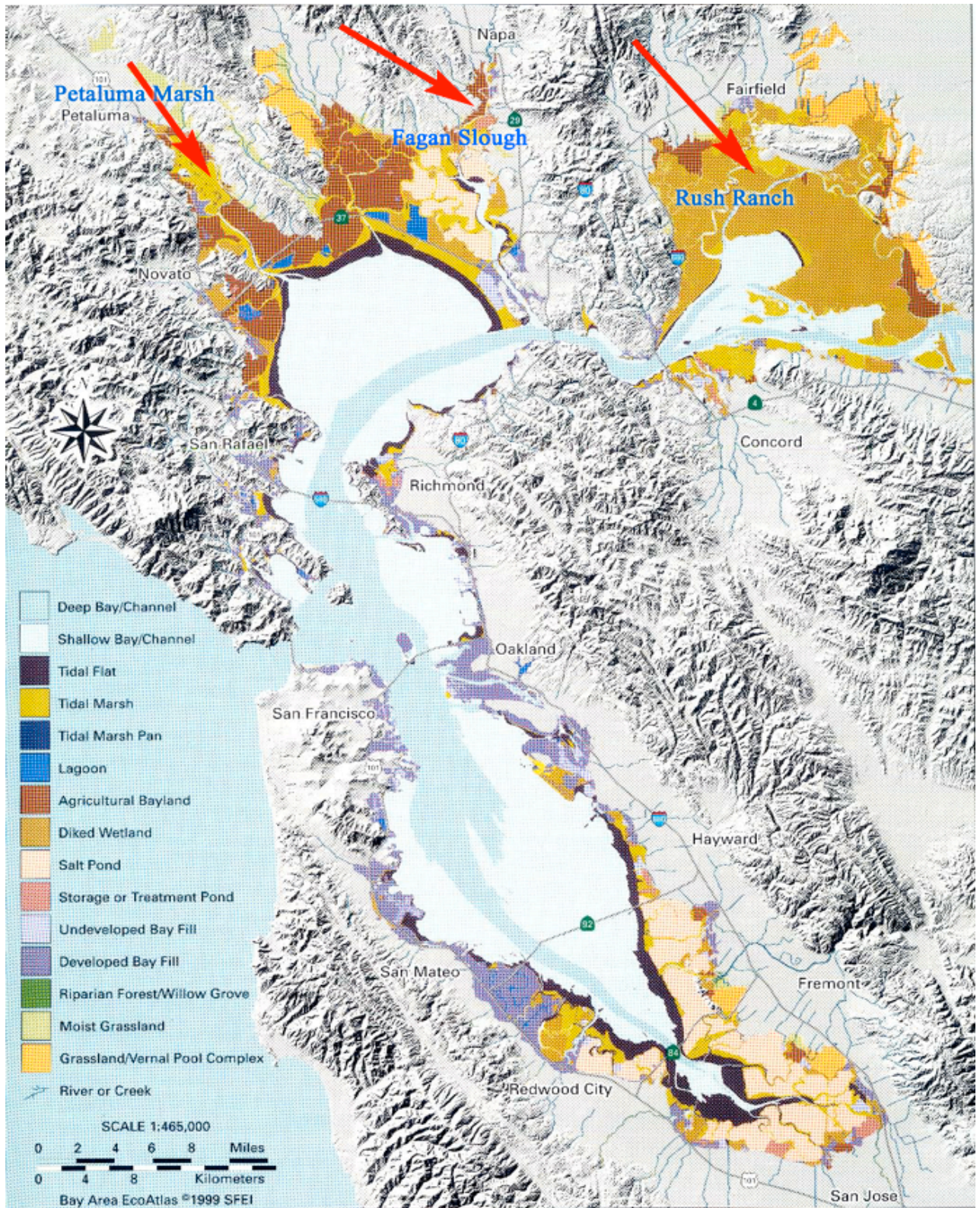


Figure 1. Map of the San Francisco Bay Estuary Ecoregion, showing location of study sites.

Figure 2. Fagan Slough soil salinities 2000-01, showing rooting zone salinity versus distance from tidal slough.

Figure 3. Results for *Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica* transplants at Fagan Slough, showing mean total biomass versus transplant zone.

Figure 4. Fagan Slough transplant mean dry weights, by zone, 2000.

Figure 5. Rush Ranch soil salinities 2000, showing rooting zone salinity versus distance from tidal slough.

Figure 6. Results for *Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica* at Rush Ranch, showing mean total biomass versus transplant zone.

Figure 7. Rush Ranch transplant mean dry weights, by zone, 2000.

Figure 8. Results for *Distichlis spicata* from mesocosm study, showing total plant biomass versus salinity and hydrology treatments.

Figure 9. Shallow-water well measurements of groundwater elevation for locations at Fagan Slough, showing location of upper water limit on various sampling dates relative to common tidal datum. Numbers in parentheses in the legend refer to distance from tidal channel.

Table 1. Native vegetation associations found within characteristic marsh zones at Fagan Slough and Rush Ranch, CA.

Table 2. ANOVA results for Fagan Slough Transplants, 2000.

ANOVA Table for Total Weight

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Species	3	1310.289	436.763	15.080	<.0001	45.239	1.000
Zone	4	410.074	102.519	3.540	.0077	14.158	.872
Species * Zone	12	900.781	75.065	2.592	.0027	31.100	.981
Residual	300	8689.081	28.964				

Table 3. ANOVA results for Rush Ranch Transplants, 2000.

ANOVA Table for Total Weight

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Species	3	3056.215	1018.738	55.670	<.0001	167.011	1.000
Zone	2	688.039	344.020	18.799	<.0001	37.599	1.000
Species * Zone	6	505.649	84.275	4.605	.0002	27.632	.991
Residual	228	4172.292	18.300				

Table 4. Results from paired t-tests of species mean response of species in transplants from Fagan Slough and Rush Ranch.

Table 5. ANOVA results for *Distichlis spicata* mesocosm treatments

ANOVA Table for Plant Grand Total

Inclusion criteria: DISP from D&D Box Corrected (imported)

	D...	Sum of Squa...	Mean Squ...	F-Va...	P-Va...	Lam...	Pow...
Status	1	9596.200	9596.200	2.92E1	<.0001	2.9E1	1.000
Flood Depth	1	5728.397	5728.397	1.74E1	<.0001	1.7E1	.993
Water Frequency	1	3300.470	3300.470	10.04	.0021	10.04	.898
Status * Flood Depth	1	28.373	28.373	.086	.7696	.086	.060
Status * Water Frequency	1	31.270	31.270	.095	.7585	.095	.061
Flood Depth * Water Frequency	1	122.379	122.379	.372	.5433	.372	.091
Status * Flood Depth * Water Frequ...	1	193.432	193.432	.588	.4451	.588	.114
Residual	#	28928.597	328.734				

Fisher's PLSD for Plant Grand Total

Effect: Status

Significance Level: 5 %

Inclusion criteria: DISP from D&D Box Corrected (imported)

	Mean Diff.	Crit. Diff.	P-Value	
No Salt, Salt	19.996	7.355	<.0001	S

Fisher's PLSD for Plant Grand Total

Effect: Flood Depth

Significance Level: 5 %

Inclusion criteria: DISP from D&D Box Corrected (imported)

	Mean Diff.	Crit. Diff.	P-Value	
1/2 Flood, Full Flood	-15.449	7.355	<.0001	S

Fisher's PLSD for Plant Grand Total

Effect: Water Frequency

Significance Level: 5 %

Inclusion criteria: DISP from D&D Box Corrected (imported)

	Mean Diff.	Crit. Diff.	P-Value	
Daily, Weekly	11.727	7.355	.0021	S

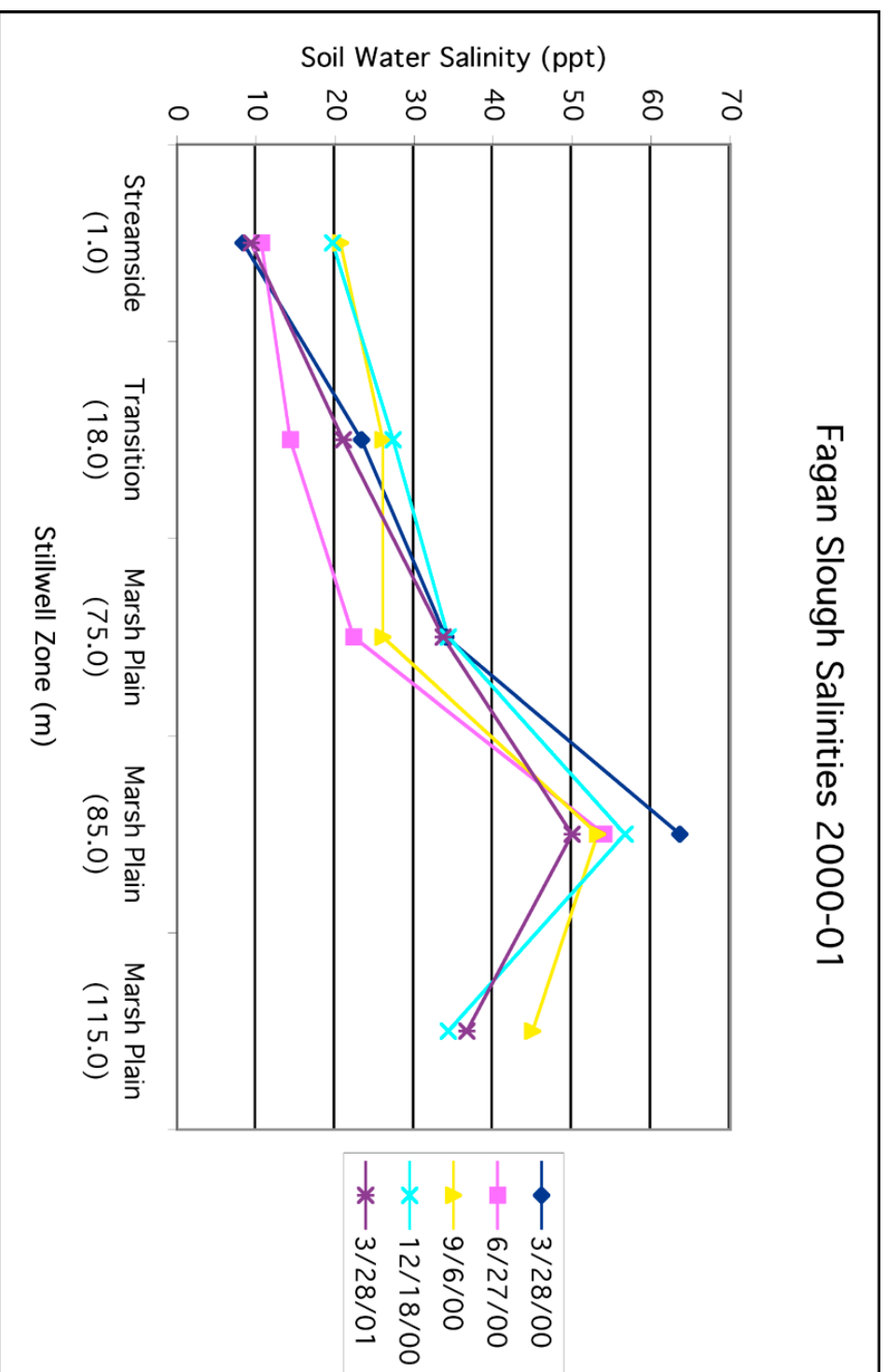


Figure 2. Fagan Slough soil salinities 2000-01, showing rooting zone salinity versus distance from tidal slough.

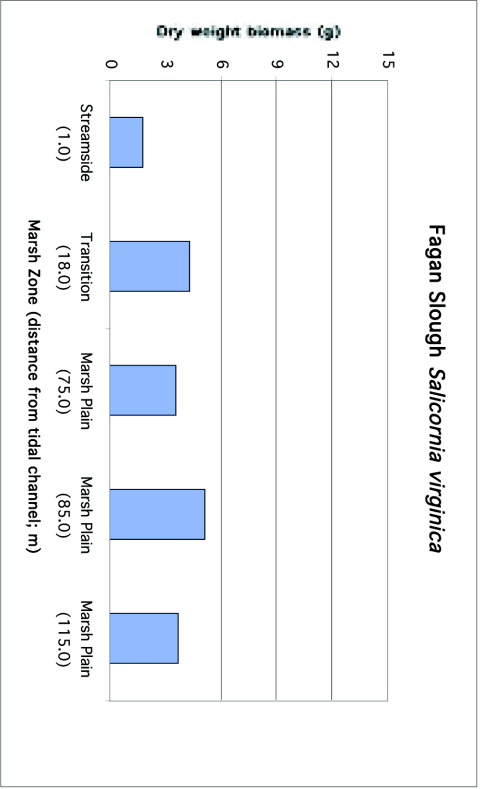
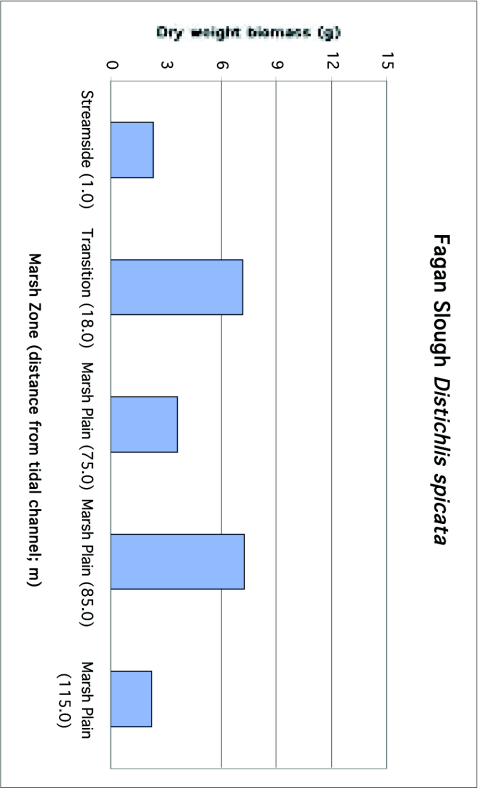
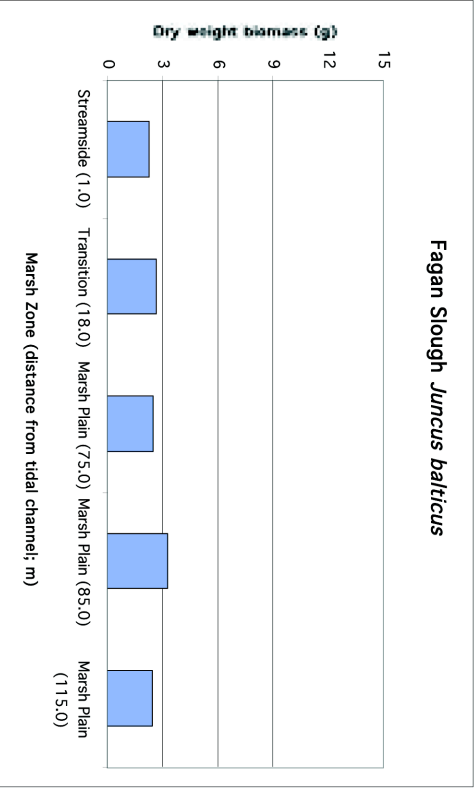
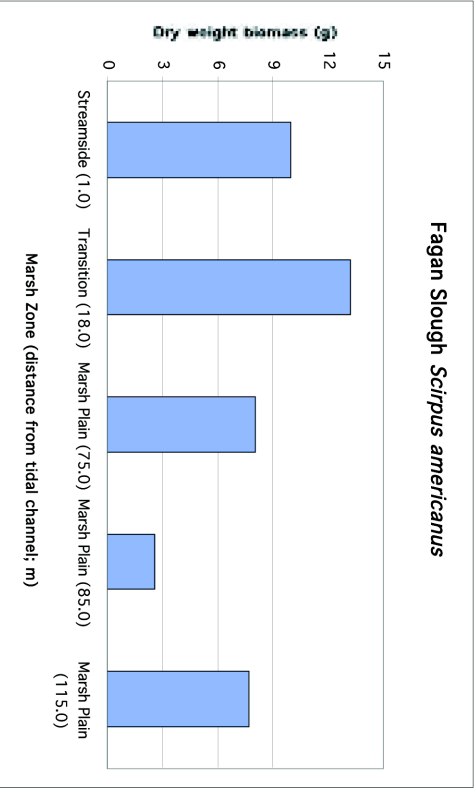


Figure 3. Results for *Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica* transplants at Fagan Slough, showing mean total biomass versus transplant zone.

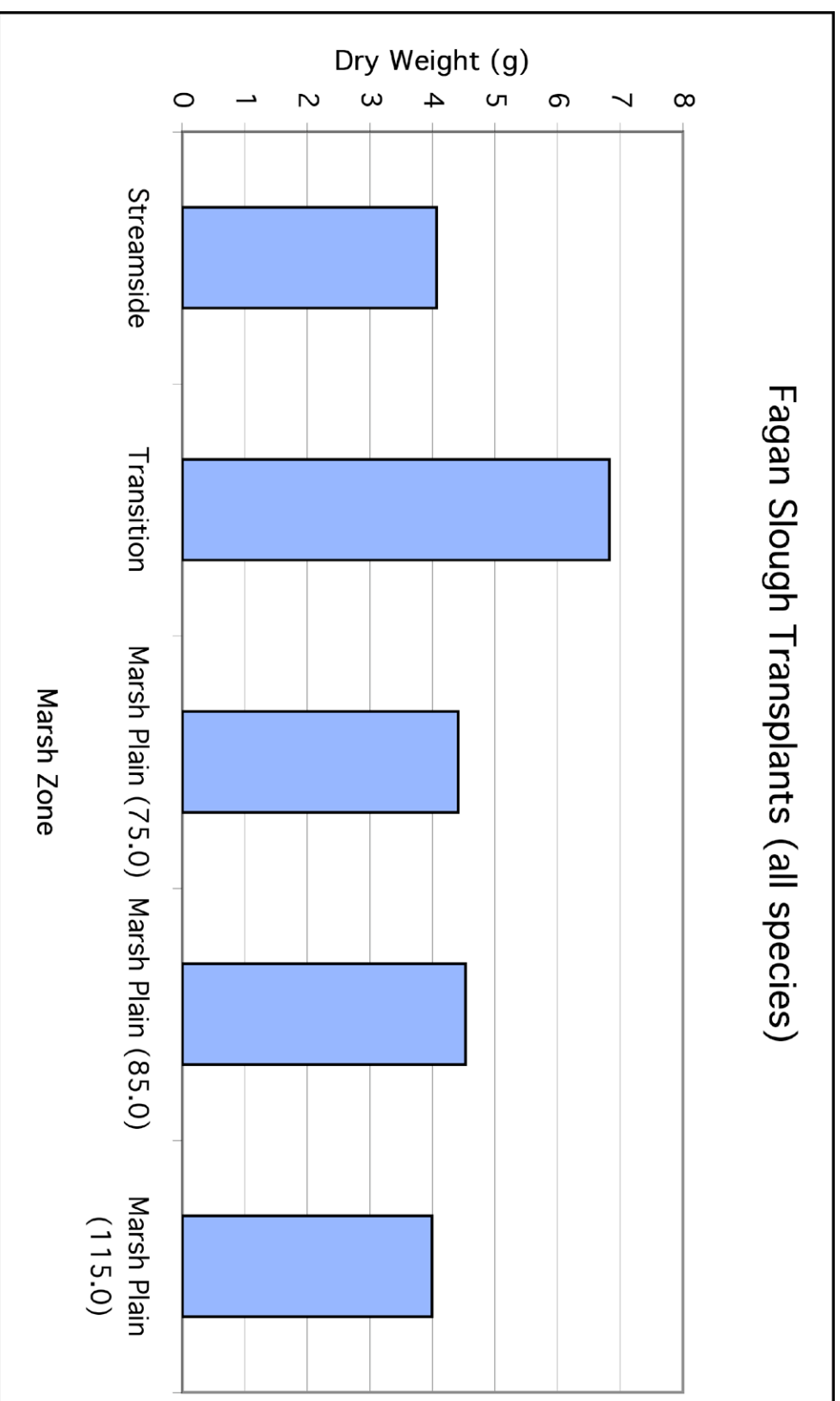


Figure 4. Fagan Slough transplant mean dry weights, by zone, 2000.

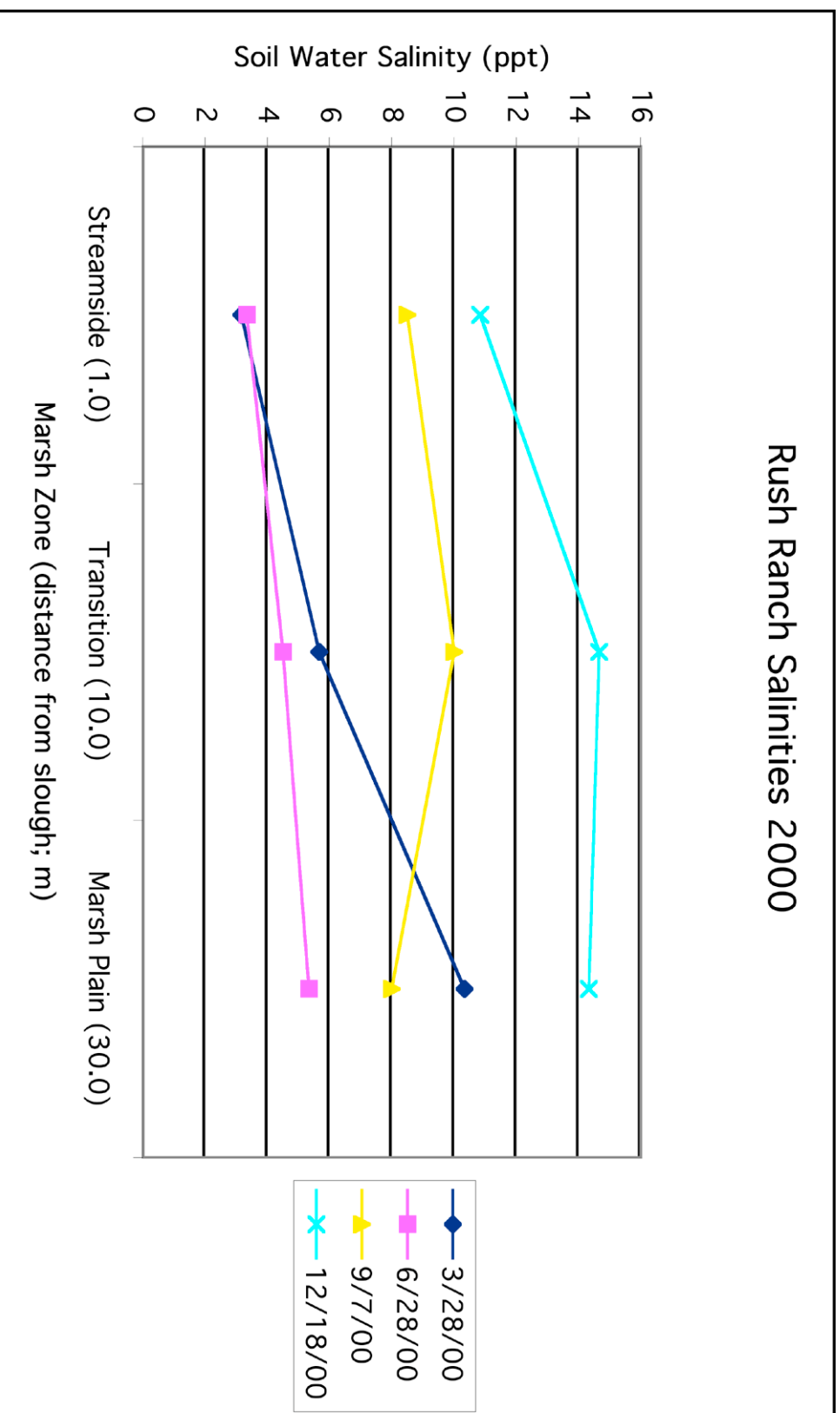


Figure 5. Rush Ranch soil salinities 2000, showing rooting zone salinity versus distance from tidal slough.

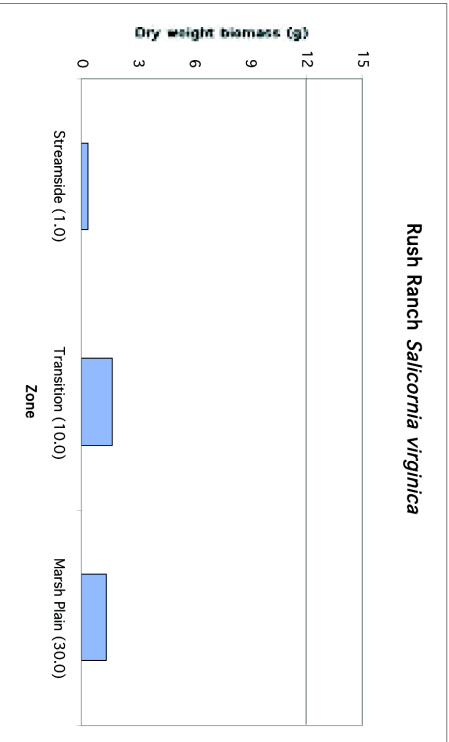
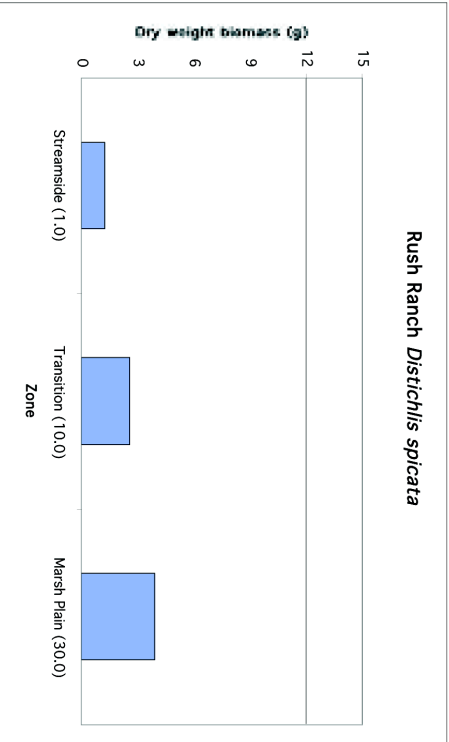
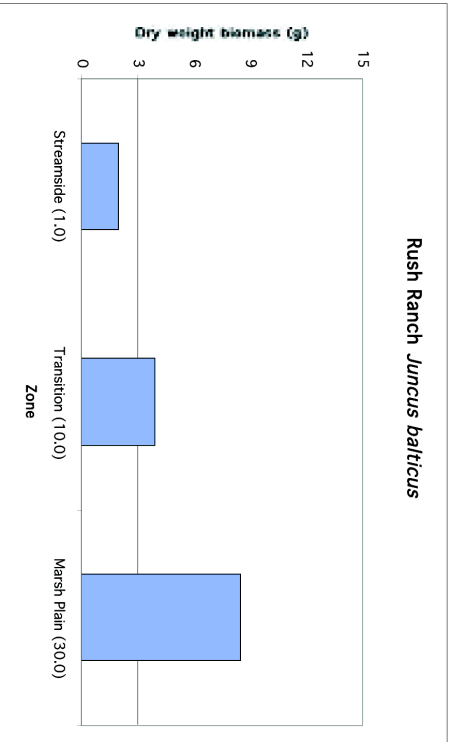
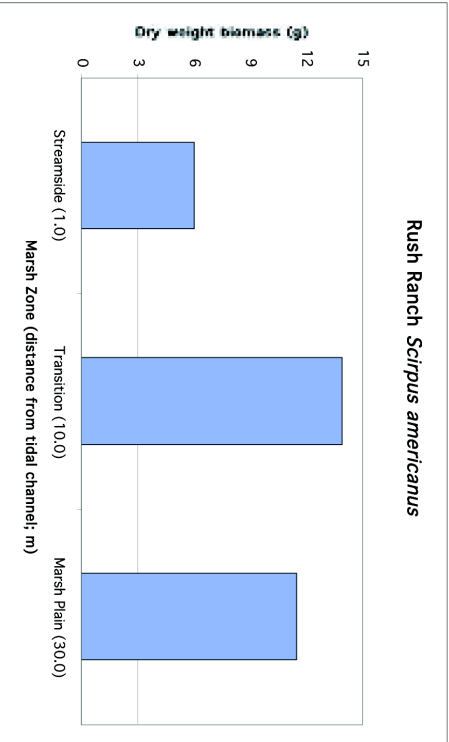


Figure 6. Results for *Scirpus americanus*, *Juncus balticus*, *Distichlis spicata*, and *Salicornia virginica* at Rush Ranch, showing mean total biomass versus transplant zone.

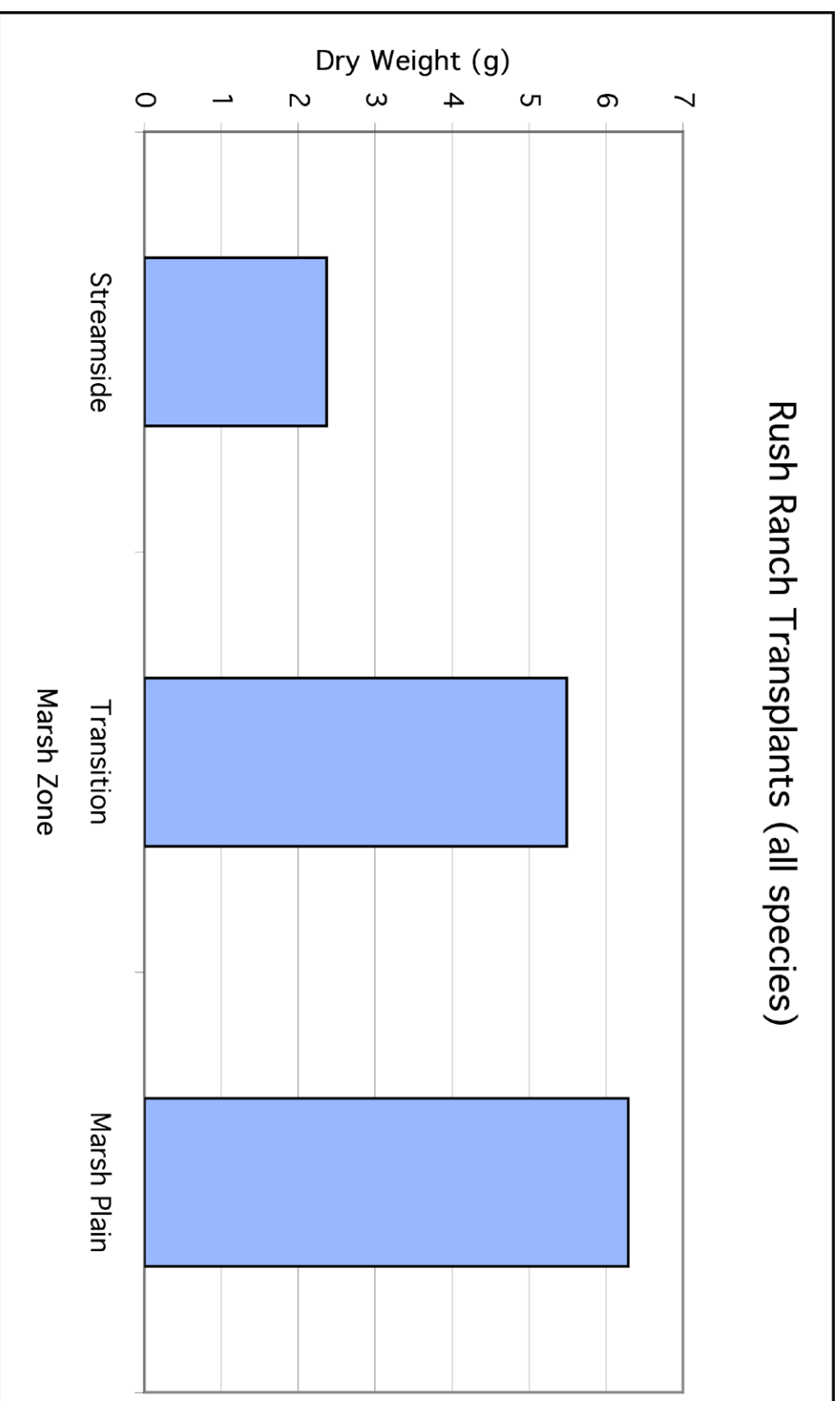


Figure 7. Rush Ranch transplant mean dry weights, by zone, 2000.

Distichlis spicata mesocosm experiment
(whole plant)

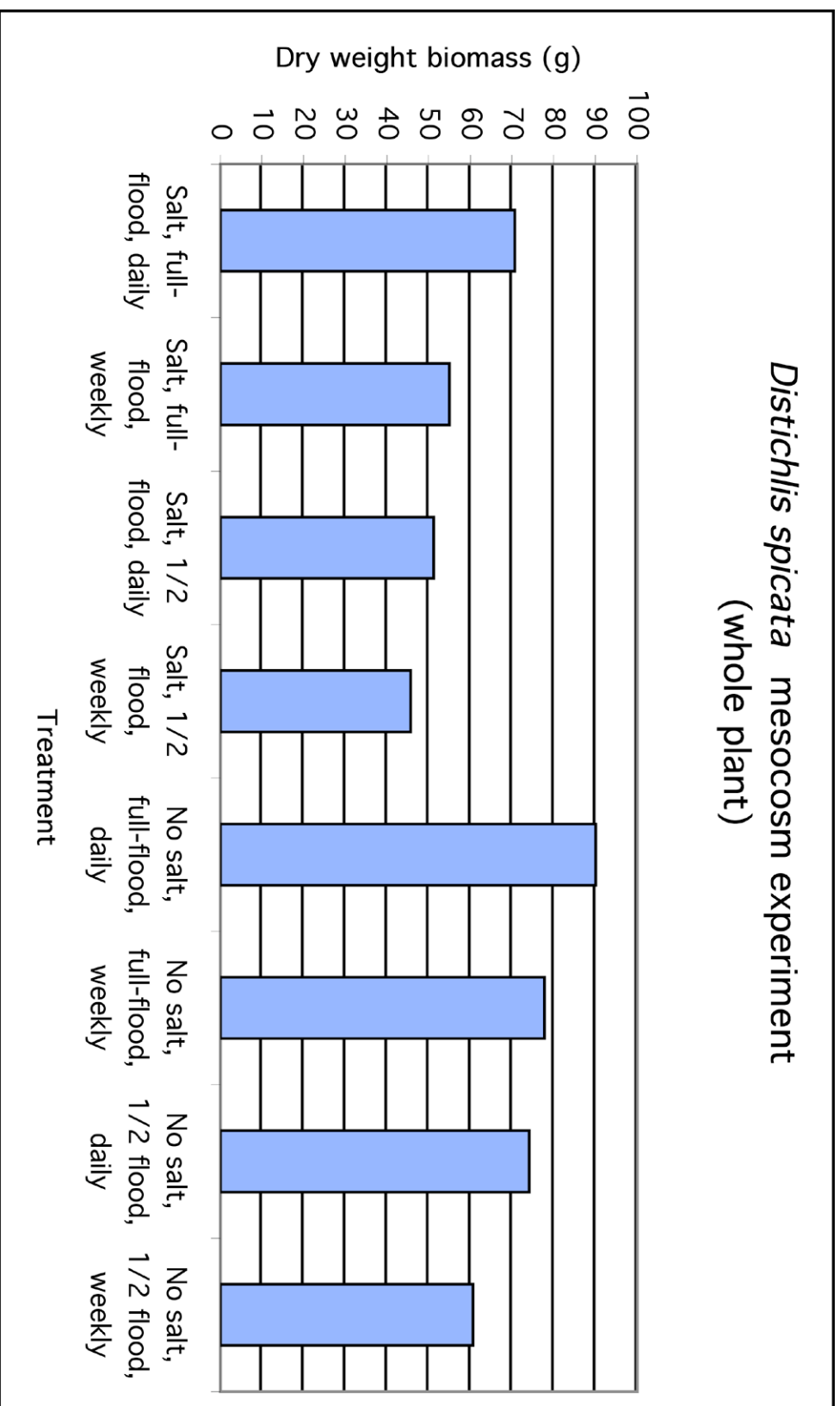


Figure 8. Results for *Distichlis spicata* from mesocosm study, showing total plant biomass versus salinity and hydrology treatments.

Groundwater Elevations (relative to common datum)

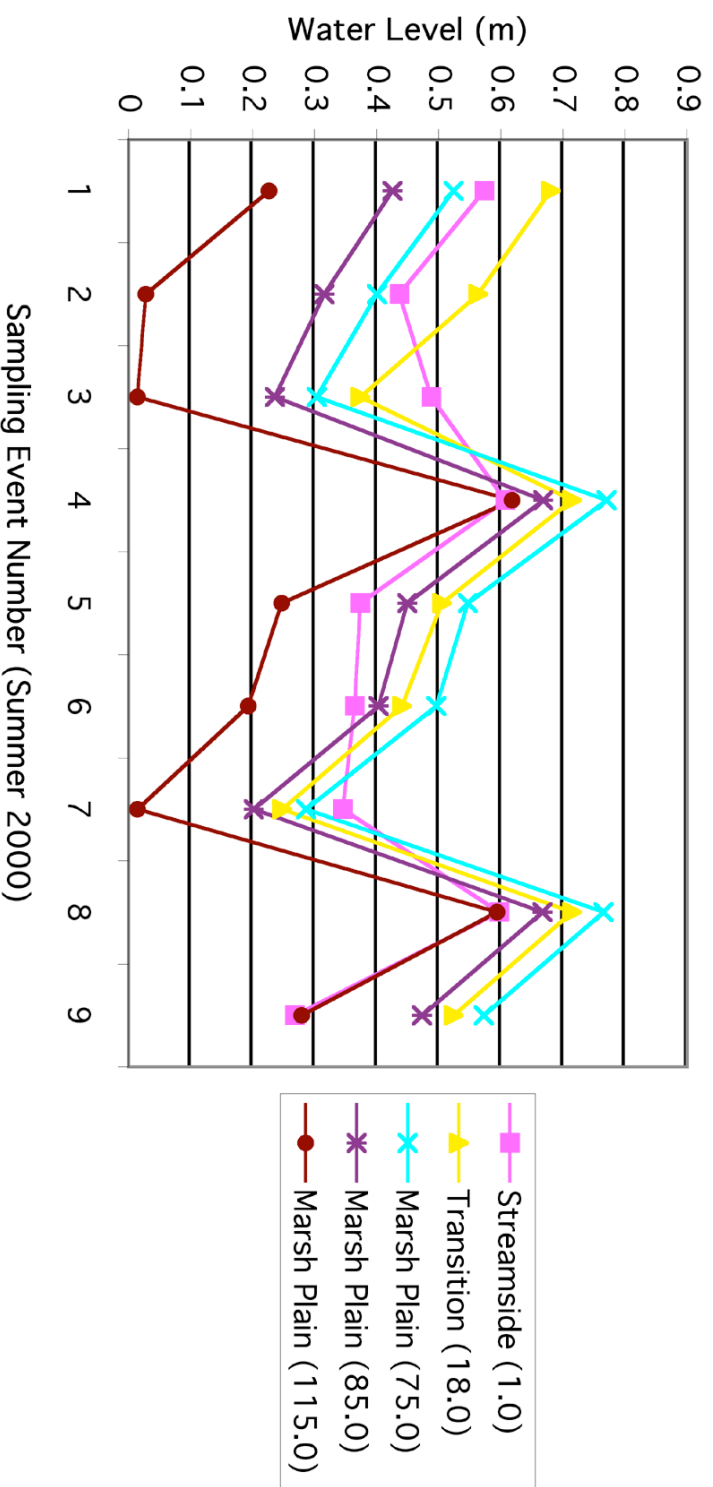


Figure 9. Shallow-water well measurements of groundwater elevation for locations at Fagan Slough, showing location of upper water limit on various sampling dates relative to common tidal datum. Numbers in parentheses in the legend refer to distance from tidal channel.

Table 1. Native vegetation associations found within characteristic marsh zones at Fagan Slough and Rush Ranch, CA.

Marsh Location	Fagan Slough Species	Rush Ranch Species
Streamside Zone	<i>Scripus acutus</i>	<i>Scripus americanus</i>
	<i>Typha latifolia</i>	<i>Apium graveolens</i>
	<i>Lepidium latifolium</i>	<i>Convolvulus arvensis</i>
	<i>Salicornia virginica</i>	
Transition Zone	<i>Juncus balticus</i>	<i>Juncus balticus</i>
	<i>Salicornia virginica</i>	<i>Scripus americanus</i>
	<i>Cuscuta salina</i>	<i>Triglochin maritima</i>
Marsh Plain	<i>Salicornia virginica</i>	<i>Distichlis spicata</i>
	<i>Cuscuta salina</i>	<i>Triglochin maritima</i>
	<i>Distichlis spicata</i>	
	<i>Juncus balticus</i>	

Table 4. Results from paired t-tests of species mean response of species in transplants from Fagan Slough and Rush Ranch.

Hypothesized difference = 0	Mean Diff.	DF	t-Value	P-Value	Significance Level
Fagan Slough, Rush Ranch: Total for all species	-1.226	239	-2.851	0.0047	**
Fagan Slough, Rush Ranch: <i>Scirpus americanus</i>	-0.068	59	-0.040	0.9683	N.S.
Fagan Slough, Rush Ranch: <i>Juncus balticus</i>	0.676	79	2.075	0.0413	*
Fagan Slough, Rush Ranch: <i>Distichlis spicata</i>	0.408	79	0.639	.5248	N.S.
Fagan Slough, Rush Ranch: <i>Salicornia virginica</i>	-4.760	79	-4.946	<0.0001	**

(** = highly significant; * = significant)

Marsh Plain Sedimentation Processes within the San Francisco Bay/Delta, CA, USA

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Abstract

Tidal marsh landscapes are complex ecosystems integrating the influence of hydrology, sediments, and vegetation as they establish and maintain their characteristic elevation and dominant plant zonation. It has been hypothesized that exogenous sedimentation is responsible for maintenance of tidal marsh elevations, mainly through the action of tidal inundation and sediment deposition. Further, it has been proposed that direct control over sedimentation rates is attributable to the nature and identity of the local, overlying vegetation. This study investigates the relationship between local sedimentation rates, identity of overlying vegetation, distance from tidal channel, and local elevation. Local sedimentation rates on marsh plains located at approximately Mean Higher High Water were found to be much lower than expected. Sedimentation rates were highest closest to tidal channels, regardless of overlying vegetation. Maintenance of tidal marsh elevations within the San Francisco Bay/Delta appears to depend as much on local productivity as on deposition of imported tidal sediments.

Introduction

Recent proposed programs of tidal marsh restoration in the San Francisco Bay/Sacramento-San Joaquin Delta Estuary (Bay/Delta Estuary) depend upon natural rates of sedimentation using existing sediment supplies and entrapment within stands of natural vegetation as a basis for re-establishment of elevations suitable for colonization by tidal marsh vegetation (Orr and Williams, 2000; Reed, 2000; Reed et al., 2000; Simenstad et al., 2000a; Simenstad et al., 2000b; Simenstad et al., 2000c; Williams et al., 2000; Collins, 2001). Previous studies have estimated the effect of tidal marsh vegetation, or simulated vegetation, on local rates of sediment accumulation under various conditions as a precursor to recommendations for tidal marsh restoration activities (Bridges and Leeder, 1976; Bayliss-Smith et al., 1979; Kesters et al., 1987; Oenema and DeLaune, 1988; Wood et al., 1989; Roig, 1994; Simenstad et al., 2000a; Day et al., 2000). Several reports have demonstrated variable sedimentation rates under

tidal marsh vegetation of different kinds (Carling 1982; Christiansen and Miller, 1983; Stumpf 1983; Clark and Patterson, 1985; Reed et al., 1985; Ashley, 1988; Reed, 1988; Nichols, 1989; Stoddart et al., 1989; Wood et al., 1989; Childers and Day, 1990; Anderson et al., 1992; Delaune et al., 1992; French and Spencer, 1993; Zwolsman et al., 1993; French et al., 1995; Leonard et al. 1995a; Boumans et al., 1997; Leonard, 1997; Dijkema, 1998; Pasternack and Brush, 1998; Yang, 1998; Anisfeld et al., 1999; Yang, 1999). While it is evident that enhancement of sedimentation may be achieved through establishment of vegetation at low tidal elevations (Mean Lower Low Water, or MLLW, for example) as precedent for restoration of marshes at lower elevations, little is known about sedimentation rates associated within existing marshes at higher elevations (Mean Higher High Water, or MHHW) within the San Francisco Bay/Delta Estuary. In other areas of North America and Europe marsh plain sedimentation is important to the maintenance of tidal marsh ecosystems (Rejmánek et al., 1988; DeLaune et al., 1990; Zwolsman et al., 1993; Cahoon and Reed, 1995, Leonard et al., 1995b). The present study has as its objective the characterization of the rates of sedimentation on two tidal marshes within the San Francisco Bay/Delta Ecoregion. The rates of sediment entrapment within existing vegetation at streamside zone, transition zone, and marsh plain locations were investigated with the intent of identifying the contribution of exogenous sediments to the soil profile found within the marsh. Differentiation of the organic and inorganic fractions of the deposited sediments was used to infer potential sources of the accumulated material. We also discuss the relative contribution of *in situ* productivity by existing marsh vegetation to the soil profile, and suggest that sedimentation in the marshes described has at least two components: 1) an exogenous, largely mineral component restricted to areas of the marsh bordering tidal channels, and; 2) a locally-produced, largely organic component which is found over a larger portion of the marsh, and which results from local productivity of existing tidal marsh vegetation. These components may differ from those found in Bay/Delta Estuary marshes found at lower tidal elevations (Simenstad et al., 2000c; Collins, 2001).

Study Location

Sediments were collected at two marshes, Fagan Slough Ecological Reserve in the Napa River drainage basin, Napa County, CA (38°13'28" N, 122°17'30" W), and at Rush Ranch in the Suisun Marsh complex, Solano County, CA (38°12'30" N, 122°2'30" W). Streamside vegetation at both sites includes *Scirpus acutus*, *Scirpus americanus*, *Typha angustifolia*, and *Lepidium latifolia*. Transition zone species are typically *Juncus balticus*, *Distichlis spicata*, and *Triglochin maritima*. *Salicornia virginica* and *Jaumea carnosa* are the common marsh plain dominants. At Fagan Slough, two watercourses were included in the study, Fagan Slough and Steamboat Slough, which fringe the Reserve. At Rush Ranch, First Mallard Branch and an associated mosquito ditch network last maintained in the 1980's (Solano County Mosquito Abatement District, personal communication, 1999) were examined.

Methods

Plastic petri dishes (70 mm diameter) fitted with glass fiber filter papers were used as sediment traps placed in various locations upon the marsh surface. Traps were affixed to the marsh surface with wire staples passed through the paper and holes drilled into each dish. Additionally, small smooth-sided glass vials (1 cm x 4.5 cm) were used as alternate sediment collection devices in order to ensure petri dishes did not allow resuspension of collected sediments over the sampling interval (Butman 1986; Butman 1986; Butman 1989). Vials were placed into the marsh soil to a depth which presented the same exposed edge height as the installed petri dishes to tidal overmarsh flows (approximately 0.5 cm height above soil surface).

Sediment trapping locations were established upon previously-existing vegetation transects within each marsh (Figures 1 and 1b). On each transect, nests of five dishes and five vials were placed within existing vegetation, spaced 25 cm apart, and oriented on an axis parallel to the nearest tidal channel. Positions of dishes and vials were established randomly along each axis. In addition to the traps placed within the marsh vegetation, 2 dishes and 2 vials were placed within an area cleared of existing vegetation along the established trap axis with at least 1 m of undisturbed vegetation between the cleared, unvegetated area and the vegetated trap area (Figure 2). Unvegetated areas were

approximately 1 m² in size. These unvegetated areas were kept clear of vegetation for the duration of the described collection periods.

A total of 27 locations were sampled at Fagan Slough (9 locations each in streamside, transition, and marsh plain locations) between August 1999 and March 2001 (567 sediment traps total). 36 locations were sampled at Rush Ranch (12 locations each streamside, transition, and marsh plain) between March 1999 and March 2001 (1260 sediment traps total). Typical vegetation associations for each zone are summarized in Table 1 (for further detail see Culberson et al., in review). Traps were recovered and processed on an approximately quarterly basis over the study period. On each collection date the traps were individually capped, removed and labeled, and replaced with new traps. Filter papers and sediments from each petri dish trap were dried at 60°C for a minimum of one week to remove water, weighed, and then ignited to 550°C to remove organic matter, and reweighed. Sediments collected in the vials were filtered onto ashless filter disks, dried at 60°C, weighed, and reweighed after ignition to 550°. All sediment weights were recorded to 0.0001 g using an analytical balance.

Data were analyzed using StatView 5.0.1 (SAS Institute Inc., Cary, NC) and ANOVA results are presented using bulk sediments collected per sampling date (g) or normalized daily rate of sedimentation (g d⁻¹), as indicated.

Results

Results from the Petri dish sediment traps and the vial sediment traps show no overall differences in sedimentation pattern, with the exception that the vials selectively excluded larger organic material from the samples (detritus, debris, shed stems, etc.) owing to their small collection orifice. Sedimentation estimates using vials were approximately 20% less than those using Petri dishes, but are otherwise similar with regard to spatial pattern. Further discussion regarding results from the vials is therefore omitted.

Fagan Slough

Daily rates of sedimentation in the streamside zone (Figure 3) averaged approximately 2.5 times the rate found further inland (15 g/m²/d versus 6 g/m²/d or less). Sediments contained progressively less inorganic material further inland (Figure 4), with

no differences in inorganic fraction of collected material due to presence or absence of vegetation (Table 3).

Examined in detail, sedimentation rates on the marsh surface at Fagan Slough are consistent with a pattern of deposition dominated by inorganic material in the streamside zone (presumably tidally-derived), and by organic material in the marsh plain zone (presumably native vegetation-derived). Collected sediments are 65-75% inorganic material (by weight) streamside, and 65-75% organic material (by weight) on the marsh plain. Transition zone inorganic:organic ratios are approximately 1.0 -- a ratio that would be expected at transitional landscape positions, where tidal and biological influences on sedimentation processes are equal (see Culberson et al., in review, for description of vegetation in each of these zones). Where there are observed differences (sampling period 1/00-8/00) in bulk sediments collected between treatments (vegetated versus unvegetated areas), the pattern is again consistent with expectations -- more sediments are collected in transitional vegetation than in unvegetated plots (through a combination of trapping of tidal sediments and *in situ* deposition of litter fall or otherwise deposited organics), and more sediments are collected in marsh plain vegetation than in unvegetated plots (perhaps via enhanced litter fall). Given that these effects are small, and are undetected within the other two sampling periods (8/99-11/99 and 11/99-1/00), we cannot assign a large role to the direct influence of litter fall from existing vegetation to sedimentation processes within the transition and marsh plain zones (at least when examined on a dry weight basis). Organic material deposited on the plates in the transition and marsh plain zones is of two types: a) bulky but lightweight leaf and stem materials from litter fall, high in carbon and water content, and; b) more granular, partially decomposed materials, deposited by tidal transport of material suspended from adjacent marsh surfaces. The latter type of material was often found within Fagan Slough transition and marsh plain zone collected sediments (S.D. Culberson, personal observation), and apparently dominates the organic sediments collected -- there were no differences in inorganic:organic ratios between vegetated and unvegetated treatments within zones (which would be expected if litter fall was an important component of the organic material collected). In the transition and marsh plain zones, sediment traps collect material with a higher proportion of organic matter than in the streamside zone,

but this material is only indirectly related to the overlying vegetation. Organic material collected in these zones does not appear to be deposited directly as litter fall, but from partially decomposed, locally-derived sources, subsequently tidally-deposited.

By contrast, organic material deposited in the streamside zone was predominantly as pieces of stems from the existing overlying vegetation (S.D. Culberson, personal observation). This material served to enhance local rates of sediment deposition through trapping, but was otherwise overwhelmed (by weight) by deposition of inorganic, tidally-transported, materials. Lack of observed differences in treatments within this zone (vegetated versus unvegetated) is due to two factors: 1) installing a small ($\sim 1 \text{ m}^2$) unvegetated area had little effect on sedimentation rates, even locally, particularly since Fagan Slough and Steamboat Slough are relatively large (3° order) tidal channels, and delivery of materials throughout the streamside zone was relatively uniform, and; 2) fallen plant materials could not easily be excluded from the unvegetated areas without also restricting tidal incursion, further reducing the effect of removing existing vegetation. In any event, as the summary in Table 3 suggests, while the streamside zone at Fagan Slough is influenced by existing vegetation (through trapping effects), the sediments captured there are largely inorganic by weight.

Rush Ranch

With one exception (sampling period 10/99-2/00), bulk sedimentation deposition phenomena at Rush Ranch are similar to those at Fagan Slough -- sedimentation in the streamside zone is higher than in the transition and marsh plain zones (Figure 5). Sediments collected streamside were 2-4 times greater than those found inland. The only collection date for which this was not found to be true comprised a sampling period that included dates of high local astronomical and meteorological tides (Winter 1999-2000), where sedimentation was found to be more uniform across the sampled marsh landscape. This is also expected more generally in contrast to Fagan Slough, since elevations at Rush Ranch are 15 – 20 cm lower (Culberson et al., in review), and therefore subjected to more frequent flooding and sedimentation during periods of higher regional tides. During these higher tides, sediments are evidently distributed more uniformly across the marsh at Rush Ranch than at Fagan Slough. These patterns were evident regardless of

experimental treatment (vegetated versus unvegetated areas) or plant species composition at the particular sediment trap location (Table 2).

Also similar to sediments collected at Fagan Slough, are several features which can be attributed to similar causes (Table 4): 1) streamside zone treatments at Rush Ranch occasionally show higher rates of bulk sediment deposition under vegetated versus unvegetated conditions; 2) transition zone treatments occasionally resulted in higher rates of sediment deposition under vegetated versus unvegetated conditions (with the exception of 3/99-5/99 sampling period, where the opposite was true, see below), and; 3) marsh plain zone treatments once resulted in higher deposition rates in vegetated versus unvegetated areas (2/00-9/00). Since no differences were observed in the inorganic/organic fractions between the sediments collected within the streamside treatments, we feel the effect of the vegetation in this zone was through zone-wide sediment trapping rather than through litter fall. In transition zone sediments at Rush Ranch, however, we find that higher bulk sedimentation found under vegetated treatments (5/99-8/99 and 2/00-9/00) in conjunction with higher inorganic fractions than in unvegetated treatments suggests that transition zone vegetation at Rush Ranch contributes more to sedimentation through sediment trapping than at Fagan Slough. This observation is consistent with lower elevations at Rush Ranch (Culberson et al, in review) which allow more frequent and more extensive tidal incursion into the transition zone, and more subsequent tidally-derived deposition in the transition zone than at Fagan Slough. The exception to this pattern found during the 3/99-5/99 sampling period occurred coincident with significant disturbance of sampling apparatus in several transition locations, presumably due to burrowing or trampling noted within the sampling areas (this disturbance was unrelated to feral pig activity noted below). Likewise, higher deposition rates in marsh plain vegetated versus unvegetated treatments (2/00-9/00) is attributable to sediment trapping effects rather than direct litter fall contribution. Without corresponding inorganic/organic fractionation results, this result is speculative, though consistent, with lower elevations and more frequent tidal incursion at Rush Ranch.

The predominant pattern of deposition dominated by tidally-derived sediments in the streamside zone, decreasing in effect with distance from tidal slough is similar to the pattern at Fagan Slough. Vegetated treatments at Rush Ranch suggest that more bulk

sediment deposition due to vegetation trapping of supplied sediments in zones other than streamside is occurring, though this effect may only be occasionally apparent and complicated by competing depositional mechanisms.

As at Fagan Slough, there is a decrease in inorganic material in collected sediments with increasing distance from tidal channel, from an average of approximately 55% streamside to 40% or less further inland (Figure 6). The one departure from this pattern was during the collection period October 1999 – February 2000, when significant disruption of the marsh surface was noted due to the action of feral pigs rooting throughout the transition and marsh plain zones (Culberson, personal observations, 1999-2000). It is notable that this was also the collection period during which sediment deposition rates were most uniform across the marsh landscape (Figure 5), indicating that feral pig activity may play a role in sediment dynamics in areas where the animals are more commonly found. Separation of feral pig disturbance effect from that of higher tides during this period was not directly investigated, and is not attempted here.

In contrast to Fagan Slough, however, is a consistent pattern of higher inorganic fraction of collected sediments in unvegetated treatments versus vegetated treatments in the transition and marsh plain zones (Table 4). The difference at Rush Ranch is attributable to lower overall elevations, but is also the product of processes occurring simultaneously which, in isolation, produce different effects (different inorganic fractions of deposited sediments). Higher bulk sedimentation with higher *organic* content of sediments collected in vegetated treatments suggests that *in situ* organic deposition is occurring in addition to sediment trapping, and may be responsible for the difference in bulk sedimentation. Lower bulk sedimentation rates in transition and marsh plain unvegetated areas indicate that the plant trapping effect is missing, but higher *inorganic* fractions in these sediments suggest that their primary source of sediment remains tidally-derived, and sedimentation is occurring in cleared areas even without trapping vegetation. This is an effect expected where flood tides occur often enough and high enough to supply sufficient sediment for deposition, but also must provide quiescent high tide conditions allowing sedimentation in areas devoid of vegetation. It is not clear whether these are conditions found uniquely at Rush Ranch, or whether they are more common at similar elevations throughout the Estuary. From our investigation, it is clear that both

biological and geomorphological processes are contributing to sedimentation patterns at both marshes. Distinction between physical and biological influences is more problematic at Rush Ranch since tidally-derived sedimentation occurs more generally across the marsh landscape at than at Fagan Slough.

Discussion

Sedimentation phenomena involving material deposited along transects located perpendicular to tidal channels in two marshes within the San Francisco Bay/Delta Estuary depend upon existing vegetation. On closer examination, the strength of this dependence varies with relative marsh elevation, marsh zone characteristics, and distance from tidal channel, and is not simply the physical process of sediment entrapment from the water column and subsequent deposition. Most tidally-transported materials are found within the streamside zone. However, deposited material from overlying vegetation plays a role in sedimentation processes in the Estuary, particularly in marshes at higher elevations that receive fewer and less frequent overmarsh tides. Litter fall is important in increasing trapping properties within stands of streamside vegetation, where fallen leaves and stems facilitate sediment retention.

Importantly, however, results from this study are limited to materials accreting onto the marsh surface, ignoring the contribution of locally-produced, largely organic material added to the soil subsurface profile through belowground plant productivity. When comparing rates of sedimentation with local intra-marsh surface elevations, we find the process of sediment deposition incapable of directly producing the elevation profiles surveyed. If the only material addition to the marsh was occurring due to exogenous, tidally-transported and deposited sources, the marsh elevational profile would develop surface profiles resembling the sedimentation rate curves discussed above (Figures 3 and 5). Elevational characterization of the marshes in this study (Culberson et al., in review) do show natural micro-berms associated with sediment deposition adjacent to the tidal channels, but otherwise reveal a fairly uniform marsh plain elevation, increasing slightly in height with distance from channel (Figure 7). Belowground productivity is contributing to the accumulation of material maintaining the marsh plain, although admittedly these results are indirect (inferring marsh elevations expected from

measured rates of sedimentation in different marsh zones, and comparing these inferred elevations to surveyed elevations). However, similar studies in the Gulf and Atlantic Coasts of North America have indeed found belowground contribution to increases in marsh surface elevation to be important (Hatton et al., 1983; Craft et al., 1993; Miller et al., 2001). Use of sediment erosion tables (SETs) in other marshes has convincingly established this method of marsh soil surface elevation change (DeLaune et al., 1990; Nyman et al., 1990; Delaune et al., 1992; Boumans and Day, 1993; Reed and Cahoon, 1993; Cahoon and Reed, 1995; Day et al., 2000; Simenstad et al., 2000c).

Our own studies of the productivity of tidal marsh vegetation show that belowground productivity can equal aboveground productivity on a seasonal basis (Culberson et al., in review; R.O. Spenst, personal communication). In the higher marsh plain landscapes examined during this study, we feel that vegetation-based elevation maintenance (through belowground organic additions to the soil column) is crucial to the longer-term persistence of the marsh landscape in the absence of widespread exogenous sediment deposition, particularly in marsh plain areas farther from tidal channel influence. This process is different than the one maintaining Gulf Coast and East Coast marshes at lower elevations (Flessa et al., 1977; Harrison and Bloom, 1977; Stumpf, 1983; Morris and Bowden, 1986; Kusters et al., 1987; Ashley, 1988; Reed, 1988; Rejmanek et al., 1988; Wood et al., 1989; DeLaune et al., 1990; Reed, 1992; Leonard et al., 1995; Boumans et al., 1997; Leonard, 1997; Reed et al., 1997; Pasternack and Brush, 1998), where vegetation trapping of tidally-transported materials contributes significantly to marsh surface elevations. At lower elevations (particularly in marshes below mean high water, with substantial stands of *Spartina* spp. or *Scirpus* spp.), vegetation trapping of imported sediments is important to accretion and marsh elevation maintenance processes, and sediments are characteristically more inorganic in composition (Reed and Cahoon, 1993; Larsson, 1996; Simenstad et al., 2000c; Miller et al., 2001). At higher elevations, such as at Fagan Slough and on the marsh plain at Rush Ranch, sedimentation trapping contributes less to surface elevation maintenance, and sediments are characteristically more organic. In these latter situations *in situ* plant productivity is important to maintaining marsh surface elevations through belowground biomass additions to the existing soil profile.

Acknowledgments

The authors would like to thank the U.S. Fish and Wildlife Service, the California Department of Fish and Game, and the Solano County Farmlands and Open Space Foundation for permission and access to study sites described in this paper. Thanks to Michael Singer, Emilo Laca and Ganga Deo for laboratory facilities and advice. Mary Pakenham-Walsh, Renee Spenst, Steve McComb, Elisabetta Lambertini, and Lina Sorensson provided valuable laboratory assistance. This paper is funded by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA66RG0477, project number R/CZ-154 through the California Sea Grant College System, and in part by the California State Resources Agency. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies. The U.S. Government is authorized to reproduce and distribute for governmental purposes.

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Figure 1a. Aerial photograph showing locations of vegetation transects/sediment trap locations at Fagan Slough, CA.

Figure 1b. Aerial photograph showing locations of vegetation transects/sediment trap locations at Rush Ranch, CA.

Figure 2. Diagram showing the placement of sediment traps (dishes or vials) within each of three vegetation zones along established transects in each marsh.

Figure 3. Fagan Slough sedimentation rates, 8/99 – 8/00.

Figure 4. Fagan Slough sediments' inorganic fractions, 8/99 – 8/00.

Figure 5. Rush Ranch sedimentation rates, 3/99 – 9/00.

Figure 6. Rush Ranch sediments' inorganic fractions, 3/99 – 9/00.

Figure 7. Average elevation profiles for vegetation transects at Rush Ranch and Fagan Slough (calibrated using slack high tide).

Table 1. Summary of vegetation associations typical of three zones in each of the study marshes.

Table 2. Species composition for each sediment trap sampling location for each marsh indicated.

Table 3. Summary of sedimentation characteristics for Fagan Slough (Fisher's PLSD for dry weight).

Table 4. Summary of sedimentation characteristics for Rush Ranch (Fisher's PLSD for dry weight).



Figure 1a. Aerial photograph showing locations of vegetation transects/sediment trap locations at Fagan Slough, CA.



Figure 1b. Aerial photograph showing locations of vegetation transects/sediment trap locations at Rush Ranch, CA.

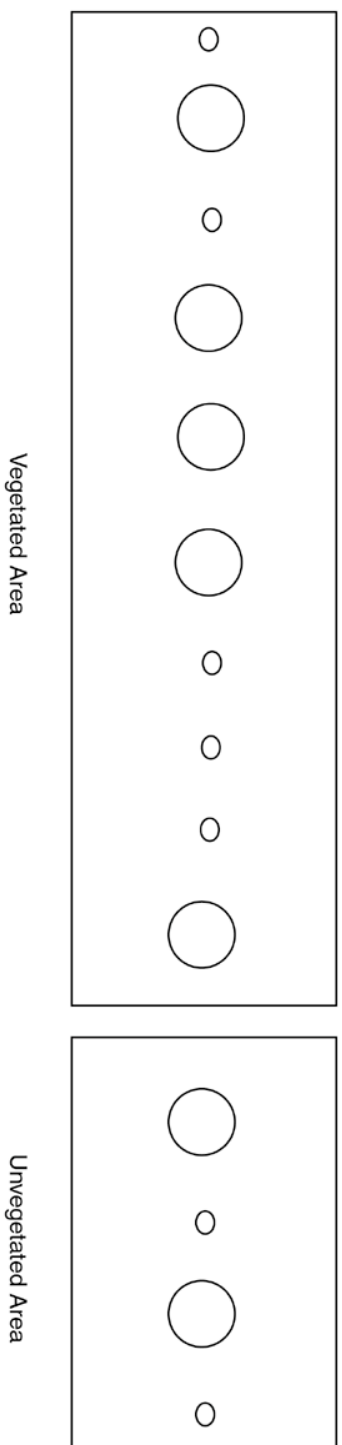


Figure 2. Diagram showing the placement of sediment traps (dishes or vials) within each of three vegetation zones along established transects in each marsh.

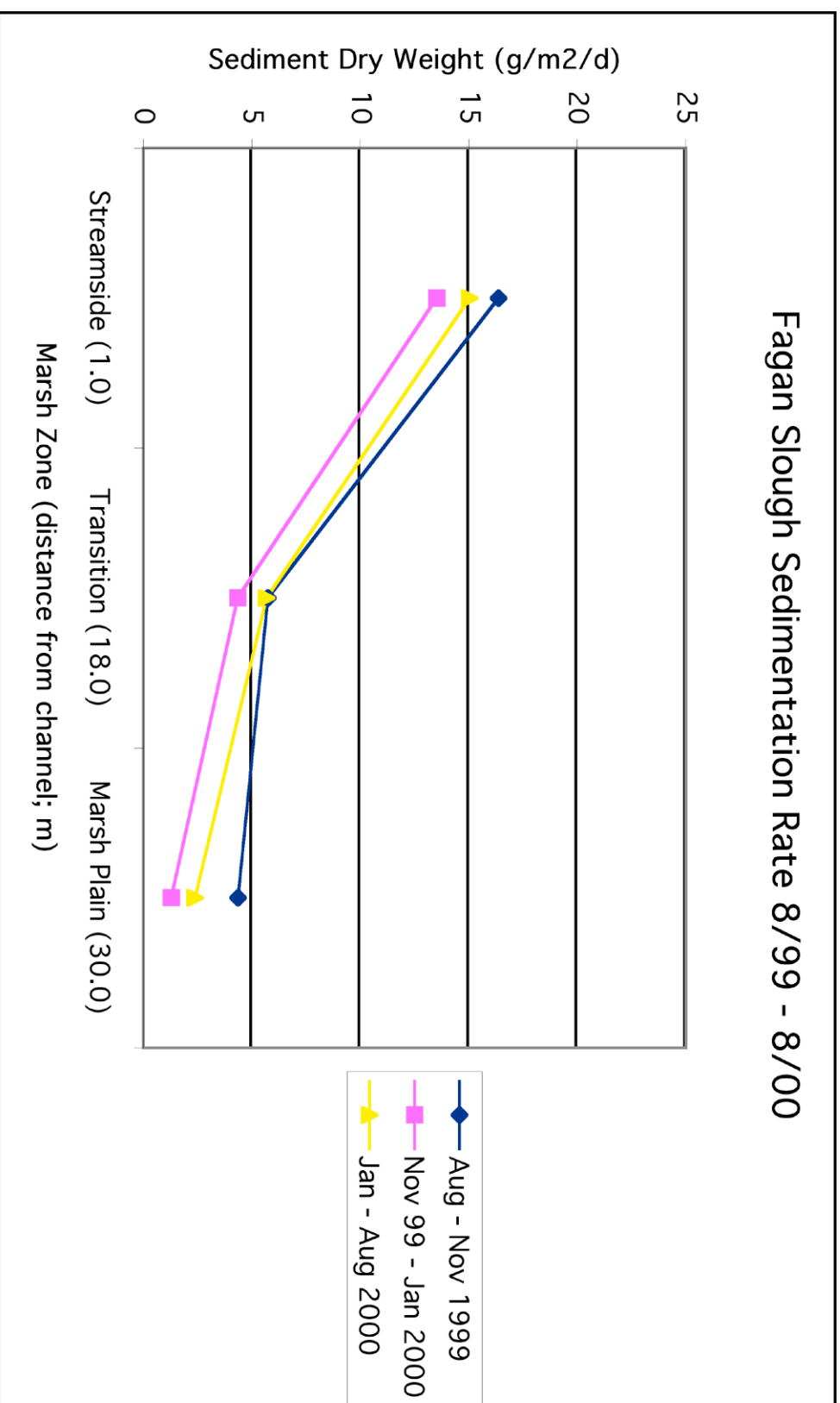


Figure 3. Fagan Slough sedimentation rates, 8/99 – 8/00.

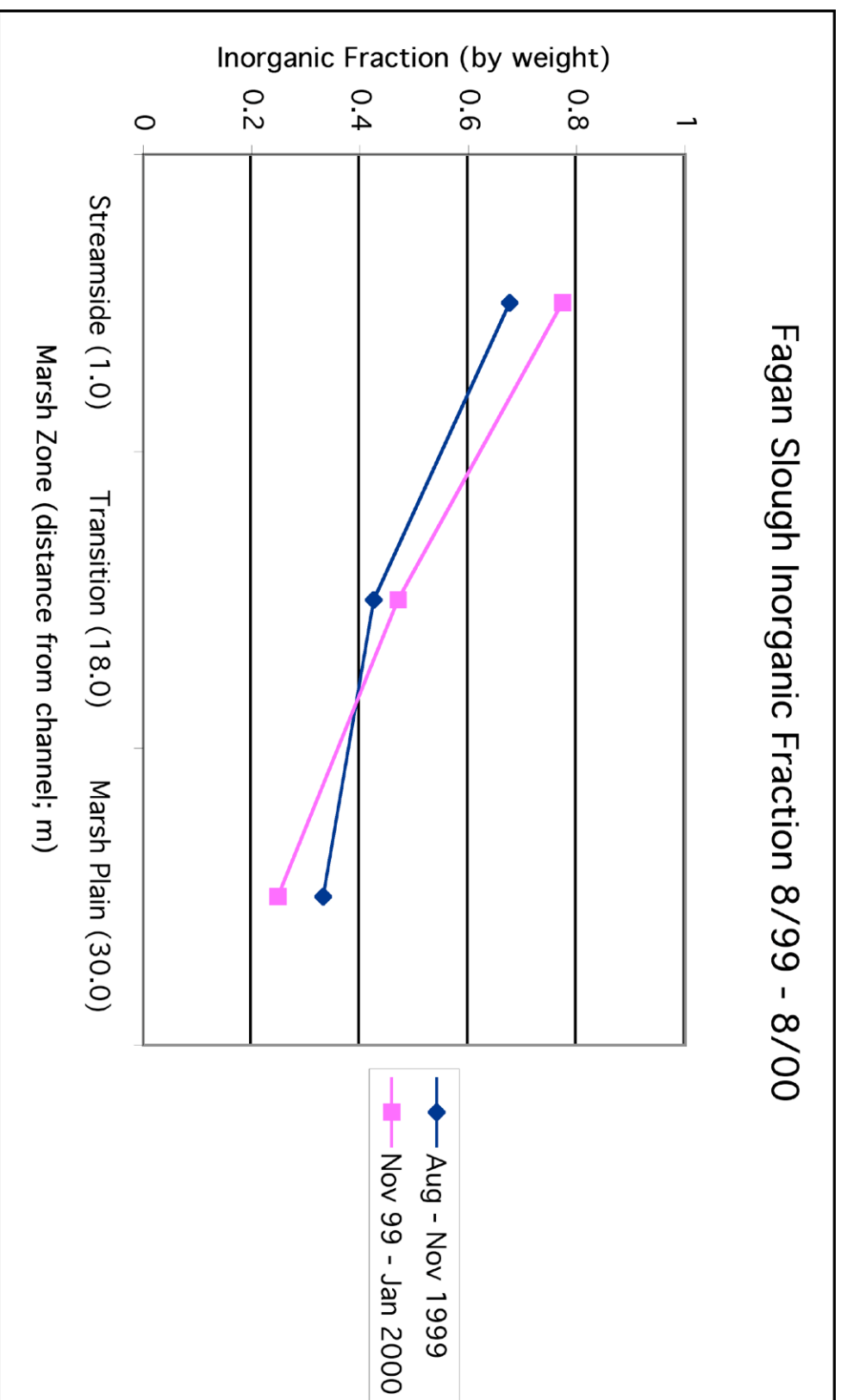


Figure 4. Fagan Slough sediments' inorganic fractions, 8/99 – 8/00.

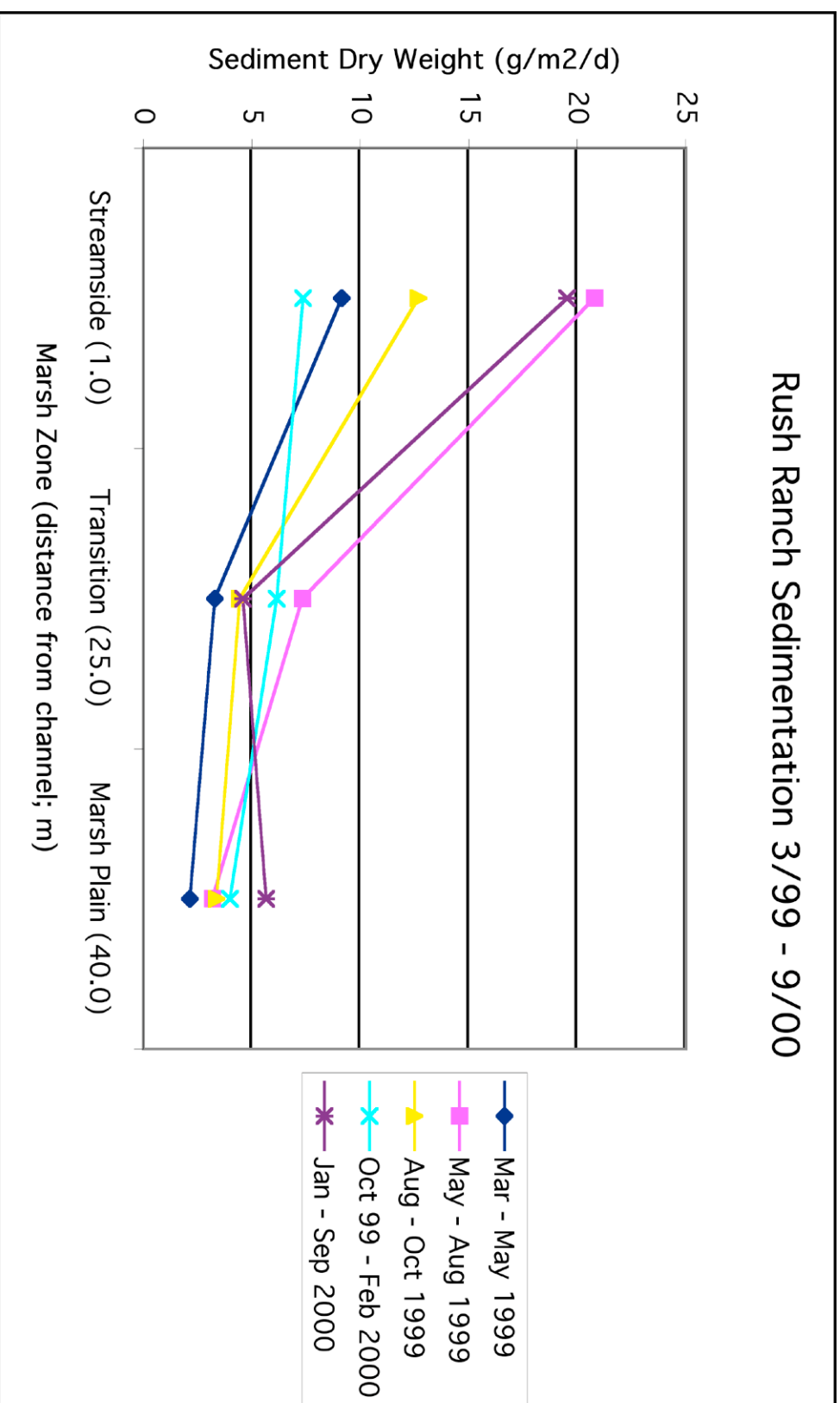


Figure 5. Rush Ranch sedimentation rates, 3/99 – 9/00.

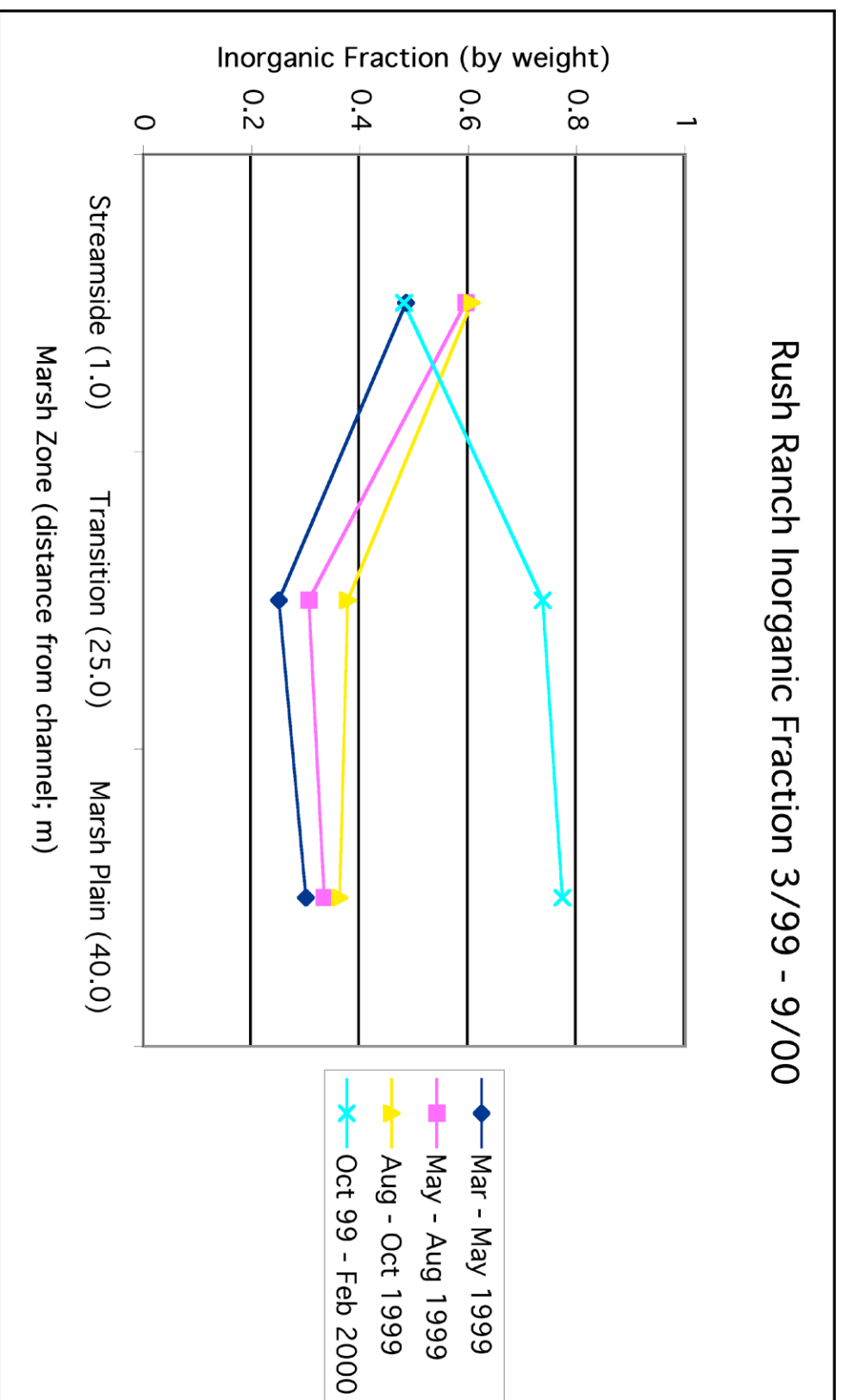


Figure 6. Rush Ranch sediments' inorganic fractions, 3/99 – 9/00.

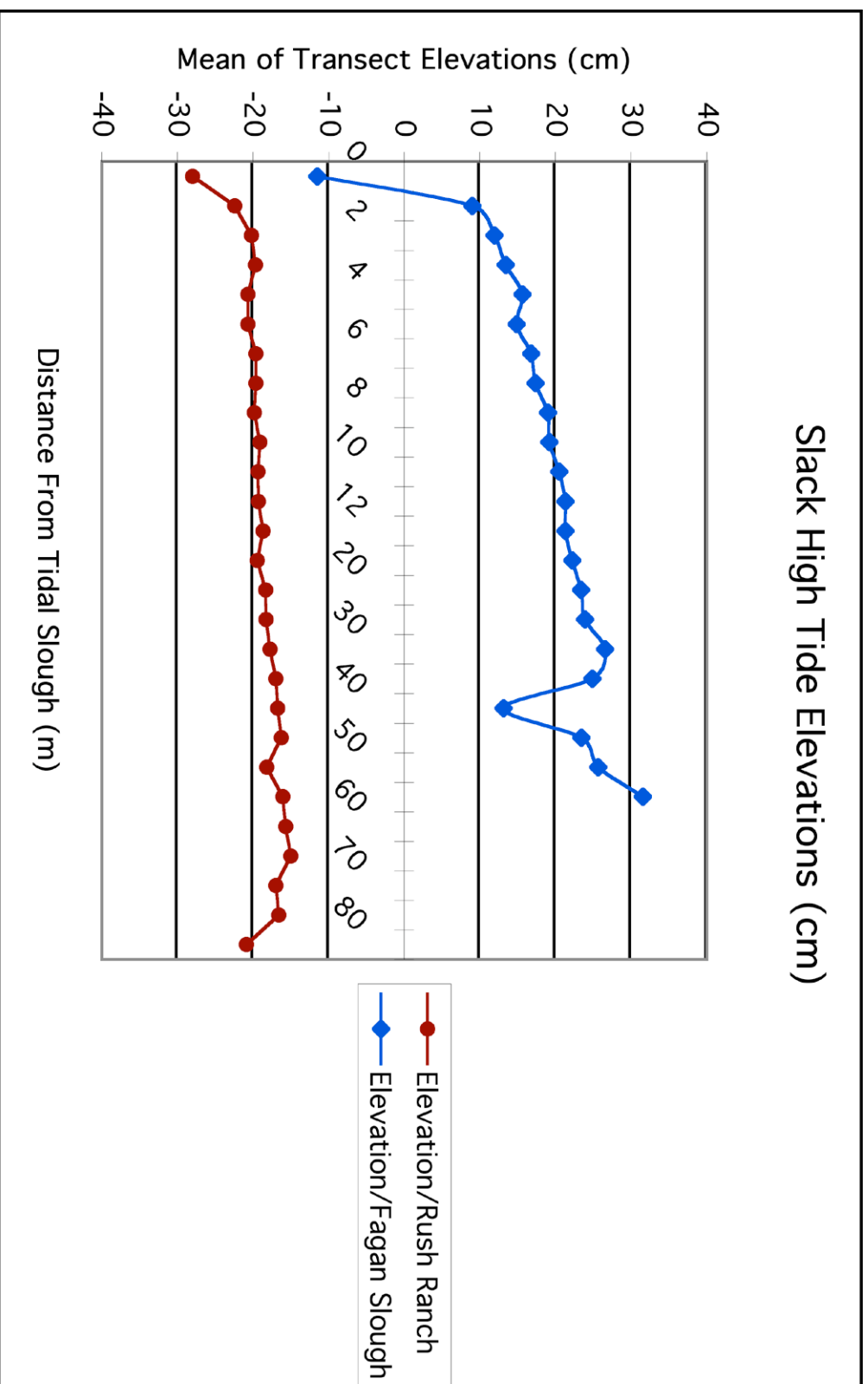


Figure 7. Average elevation profiles for vegetation transects at Rush Ranch and Fagan Slough (calibrated using slack high tide).

Table 2. Species composition for each sediment trap sampling location for each marsh indicated.

Rush Ranch	
<u>Sediment Trap</u>	<u>Species composition</u>
1.	<i>Typha angustifolia</i> , <i>Potentilla anserina</i> , <i>Juncus balticus</i> , <i>Apium graveolens</i> , <i>Grindelia stricta</i>
2.	<i>Scirpus americanus</i> , <i>Atriplex triangularis</i> , <i>Triglochin maritima</i> , <i>Salicornia virginica</i> , <i>Distichlis spicata</i>
3.	<i>Salicornia virginica</i> , <i>Distichlis spicata</i>
4.	<i>Potentilla anserina</i> , <i>Scirpus americanus</i> , <i>Juncus balticus</i> , <i>Grindelia stricta</i>
5.	<i>Juncus balticus</i> , <i>Atriplex triangularis</i> , <i>Salicornia virginica</i> , <i>Distichlis spicata</i>
6.	<i>Salicornia virginica</i> , <i>Jaumea carnosa</i> , <i>Distichlis spicata</i> , <i>Cuscuta salina</i>
7.	<i>Typha angustifolia</i> , <i>Scirpus acutus</i> , <i>Scirpus americanus</i> , <i>Lepidium latifolium</i> , <i>Scirpus californicus</i> , <i>Convolvulus arvensis</i>
8.	<i>Potentilla anserina</i> , <i>Scirpus americanus</i> , <i>Juncus balticus</i> , <i>Atriplex triangularis</i> , <i>Glaux maritima</i> , <i>Jaumea carnosa</i> , <i>Distichlis spicata</i>
9.	<i>Potentilla anserina</i> , <i>Juncus balticus</i> , <i>Atriplex triangularis</i> , <i>Glaux maritima</i> , <i>Triglochin maritima</i> , <i>Jaumea carnosa</i>
10.	<i>Potentilla anserina</i> , <i>Scirpus americanus</i> , <i>Juncus balticus</i>
11.	<i>Apium graveolens</i> , <i>Atriplex triangularis</i> , <i>Glaux maritima</i> , <i>Distichlis spicata</i> , <i>Grindelia stricta</i>
12.	<i>Atriplex triangularis</i> , <i>Salicornia virginica</i> , <i>Distichlis spicata</i>
13.	<i>Typha angustifolia</i> , <i>Scirpus acutus</i> , <i>Scirpus americanus</i> , <i>Juncus balticus</i>
14.	<i>Potentilla anserina</i> , <i>Scirpus americanus</i> , <i>Juncus balticus</i> , <i>Triglochin maritima</i> , <i>Salicornia virginica</i> , <i>Jaumea carnosa</i> , <i>Distichlis spicata</i>
15.	<i>Potentilla anserina</i> , <i>Juncus balticus</i> , <i>Triglochin maritima</i> , <i>Jaumea carnosa</i> , <i>Distichlis spicata</i>
16.	<i>Typha angustifolia</i> , <i>Scirpus acutus</i>
17.	<i>Potentilla anserina</i> , <i>Scirpus americanus</i> , <i>Juncus balticus</i> , <i>Triglochin maritima</i> , <i>Jaumea carnosa</i> , <i>Distichlis spicata</i>
18.	<i>Potentilla anserina</i> , <i>Juncus balticus</i> , <i>Atriplex triangularis</i> , <i>Triglochin maritima</i> , <i>Jaumea carnosa</i> , <i>Distichlis spicata</i> , <i>Grindelia stricta</i>
19.	<i>Potentilla anserina</i> , <i>Scirpus americanus</i> , <i>Scirpus californicus</i> , <i>Convolvulus arvensis</i>
20.	<i>Potentilla anserina</i> , <i>Scirpus americanus</i> , <i>Juncus balticus</i> , <i>Triglochin maritima</i>

21. *Scirpus americanus*, *Juncus balticus*, *Triglochin maritima*, *Salicornia virginica*, *Jaumea carnosa*, *Distichlis spicata*
22. *Typha angustifolia*, *Potentilla anserina*, *Convolvulus arvensis*
23. *Potentilla anserina*, *Juncus balticus*, *Glaux maritima*, *Triglochin maritima*, *Jaumea carnosa*, *Distichlis spicata*
24. *Juncus balticus*, *Atriplex triangularis*, *Glaux maritima*, *Triglochin maritima*, *Jaumea carnosa*, *Distichlis spicata*
25. *Typha angustifolia*, *Potentilla anserina*
26. *Typha angustifolia*, *Potentilla anserina*, *Scirpus americanus*
27. *Potentilla anserina*, *Scirpus americanus*
28. *Potentilla anserina*, *Scirpus americanus*, *Juncus balticus*
29. *Potentilla anserina*, *Scirpus americanus*, *Juncus balticus*
30. *Juncus balticus*, *Atriplex triangularis*, *Jaumea carnosa*, *Distichlis spicata*
31. *Scirpus americanus*, *Juncus balticus*, *Apium graveolens*, *Polygonum* sp.
32. *Potentilla anserina*, *Scirpus americanus*, *Juncus balticus*, *Glaux maritima*, *Triglochin maritima*, *Jaumea carnosa*, *Distichlis spicata*
33. *Potentilla anserina*, *Juncus balticus*, *Glaux maritima*, *Triglochin maritima*, *Jaumea carnosa*, *Distichlis spicata*
34. *Potentilla anserina*, *Scirpus americanus*, *Juncus balticus*, *Glaux maritima*, *Triglochin maritima*, *Jaumea carnosa*, *Distichlis spicata*, *Grindelia stricta*
35. *Juncus balticus*, *Apium graveolens*, *Triglochin maritima*, *Salicornia virginica*, *Jaumea carnosa*, *Distichlis spicata*, *Grindelia stricta*
36. *Juncus balticus*, *Atriplex triangularis*, *Glaux maritima*, *Triglochin maritima*, *Salicornia virginica*, *Distichlis spicata*

Fagan Slough

Sediment Trap

1. Species composition
Scirpus acutus, *Scirpus americanus*, *Scirpus californicus*, *Apium graveolens*, *Salicornia virginica*
2. *Potentilla anserina*, *Juncus balticus*, *Salicornia virginica*, *Distichlis spicata*
3. *Atriplex triangularis*, *Salicornia virginica*, *Cuscuta salina*
4. *Scirpus americanus*, *Lepidium latifolium*, *Limonium californicus*, *Typha latifolia*
5. *Potentilla anserina*, *Lepidium latifolium*, *Juncus balticus*, *Atriplex triangularis*
6. *Salicornia virginica*, *Cuscuta salina*
7. *Lepidium latifolium*, *Juncus balticus*, *Salicornia virginica*

8. *Lepidium latifolium*, *Juncus balticus*, *Salicornia virginica*
9. *Salicornia virginica*
10. *Scirpus americanus*, *Salicornia virginica*, *Scirpus maritima*
11. *Potentilla anserina*, *Juncus balticus*, *Salicornia virginica*
12. *Salicornia virginica*, *Baccharis douglasii*
13. *Scirpus americanus*, *Lepidium latifolium*, *Salicornia virginica*, *Scirpus maritima*
14. *Scirpus americanus*, *Salicornia virginica*, *Scirpus maritima*
15. *Salicornia virginica*
16. *Scirpus acutus*, *Lepidium latifolium*, *Salicornia virginica*, *Scirpus maritima*
17. *Potentilla anserina*, *Scirpus americanus*, *Juncus balticus*, *Salicornia virginica*, *Distichlis spicata*
18. *Salicornia virginica*, *Cuscuta salina*
19. *Lepidium latifolium*, *Scirpus californicus*, *Salicornia virginica*, *Scirpus maritima*
20. *Potentilla anserina*, *Scirpus americanus*, *Salicornia virginica*
21. *Potentilla anserina*, *Juncus balticus*, *Salicornia virginica*
22. *Scirpus acutus*, *Lepidium latifolium*, *Salicornia virginica*
23. *Potentilla anserina*, *Scirpus americanus*, *Juncus balticus*, *Salicornia virginica*
24. *Potentilla anserina*, *Salicornia virginica*
25. *Juncus balticus*, *Salicornia virginica*, *Scirpus maritima*
26. *Potentilla anserina*, *Juncus balticus*, *Glaux maritima*, *Salicornia virginica*, *Grindelia stricta*
27. *Salicornia virginica*, *Jaumea carnosa*, *Cuscuta salina*

Table 3. Summary of sedimentation characteristics for Fagan Slough (Fisher's PLSD for dry weight).

Fagan Slough

Whole Marsh Comparison (bulk sediments per sample period, by zone)

8/99-11/99: Streamside sediments > Transition, Marsh Plain sediments (p<0.0001)
11/99-1/00: Streamside sediments > Transition, Marsh Plain sediments (p<0.0001)
1/00-8/00: Streamside sediments > Transition, Marsh Plain sediments (p<0.0001)

Within Zone Comparison (bulk sediments per sample period, by treatment – vegetated versus unvegetated)

8/99-11/99: N.S.
11/99-1/00: N.S.
1/00-8/00: Transition Zone vegetated > unvegetated (p=0.0483), Marsh Plain Zone vegetated > unvegetated (p=0.0491)

Whole Marsh Inorganic Fraction (fraction dry weight, by zone)

9/99-11/99: Streamside Zone fraction > Transition Zone fraction > Marsh Plain Zone fraction (p<0.0019)
11/99-1/00: Streamside Zone fraction > Transition Zone fraction > Marsh Plain Zone fraction (p<0.0305)
1/00-8/00: N/A

Within Zone Inorganic Fraction (fraction dry weight, by treatment – vegetated versus unvegetated)

9/99-11-99: N.S.
11/99-1/00: N.S.
1/00-8/00: N/A

(results displayed graphically in Figure 3 and Figure 4; see text)

Table 4. Summary of sedimentation characteristics for Rush Ranch (Fisher's PLSD for dry weight).

Rush Ranch

Whole Marsh Comparison (bulk sediments per sample period, by zone)

3/99-5/99: Streamside sediments > Transition, Marsh Plain sediments (p<0.0010)
 5/99-8/99: Streamside sediments > Transition, Marsh Plain sediments (p<0.0001)
 8/99-10/99: Streamside sediments > Transition, Marsh Plain sediments (p<0.0001)
 10/99-2/00: N.S.
 2/00-9/00: Streamside sediments > Transition, Marsh Plain sediments (p<0.0001)

Within Zone Comparison (bulk sediments per sample period, by treatment – vegetated versus unvegetated)

3/99-5/99: Transition Zone unvegetated > vegetated (p=0.0432)
 5/99-8/99: Streamside Zone unvegetated < vegetated (p=0.0452), Transition Zone unvegetated < vegetated (p=0.0297)
 8/99-10/99: Streamside Zone unvegetated < vegetated (p=0.0434)
 10/99-2/00: N.S.
 2/00-9/00: Transition Zone unvegetated < vegetated (p=0.0095), Marsh Plain Zone unvegetated < vegetated (p=0.0041)

Whole Marsh Inorganic Fraction (fraction dry weight, by zone)

3/99-5/99: Streamside Zone fraction > Transition Zone, Marsh Plain Zone fraction (p<0.0001)
 5/99-8/99: Streamside Zone fraction > Transition Zone, Marsh Plain Zone fraction (p<0.0001)
 8/99-10/99: Streamside Zone fraction > Transition Zone, Marsh Plain Zone fraction (p<0.0001)
 10/99-2/00: N.S.
 2/00-9/00: N/A

Within Zone Inorganic Fraction (fraction dry weight, by treatment – vegetated versus unvegetated)

3/99-5/99: Transition Zone unvegetated > vegetated (p=0.0148), Marsh Plain unvegetated > vegetated (p<0.0001)
 5/99-8/99: Transition Zone unvegetated > vegetated (p=0.0014), Marsh Plain unvegetated > vegetated (p=0.0003)
 8/99-10/99: Transition Zone unvegetated > vegetated (p=0.0002), Marsh Plain unvegetated > vegetated (p=0.0438)
 10/99-2/00: Marsh Plain Zone unvegetated > vegetated (p=0.0381)
 2/00-9/00: N/A

Local Salinity and Regional Restoration – Concluding Remarks

Summary of Findings

Chapter 1, “The Relative Influence of Tidal Hydrology and Soil Salinity on Canopy Dominance in Marsh Vegetation of the San Francisco Bay Estuary,” detailed the nature of vegetation zonation within three marshes in the Estuary and characterized the influence of salinity on this zonation. Tidal channel influence on vegetation decreases in extent as the Golden Gate/Pacific Ocean is approached in the ecoregion. This effect is related to regional salinity patterns in the tides reaching the studied marshes through regulation of local soil salinity. Soil salinity was found to be important for structuring tidal marsh vegetation, dependant on geographical position within the Estuary.

In chapter 2, “Experimental Verification of Soil Salinity as the Dominant Control of Vegetation Productivity in Tidal Marshes of the San Francisco Bay Estuary,” experimental methods were used to determine the effect of salinity and water availability on selected marsh plant species’ productivity. These results were examined to determine the proximate casual mechanism of vegetation zonation patterns found in experimental treatments and existing tidal marsh vegetation. Where salinity stress was low, competition controlled plant productivity; under salt stress, salinity and water availability determined biomass accumulation.

Sedimentation phenomena were described in chapter 3. “Marsh Plain Sedimentation Processes within the San Francisco Bay/Delta, CA, USA.” The role of existing tidal marsh vegetation in the higher marshes of the Estuary was examined to determine the extent to which it traps incoming sediment. Trapped imported sediments contributed to maintenance of marsh elevations in the streamside zone, but this sediment capture did not account for increasing elevations further inland. Tidal marsh primary productivity was presumed to be important to the maintenance of marsh plain elevations away from the immediate streamside zone of sediment capture.

Postscript

Tidal marsh landscapes are complex environments integrating variable biological and physical influences at the interface between terrestrial and marine ecosystems. Where riverine inputs establish estuaries, precipitation and runoff patterns further subject tidal marshes to climatic and meteorological forces. The studies detailed within this dissertation sought to identify the nature and magnitude of hydrologic factors on the patterns of vegetation and sedimentation/accretion within the San Francisco Bay/Delta Estuary, and show that the strength of these factors depends upon location within regional salinity gradients. This hydrologic influence has been examined directly through its control of soil pore water salinity and sediment deposition, and indirectly through expression as primary productivity by tidal marsh vegetation. By comparing characteristics of tidal marshes at three locations along the salinity gradient from Suisun Marsh to San Pablo Bay, CA, the underlying effect of increasing soil salinity on the zonation of tidal marsh vegetation has been identified. The conceptual model of zonation offered, which incorporates local effects of regional salinity patterns, accounts for local differences in vegetation zonation while retaining regional applicability. In addition, through selection of marshes occupying the higher reaches of tidal incursion (Mean High Water and above), contrasts between sedimentation/accretion processes in these marshes versus those found lower in the tidal range frequently discussed in the estuary/tidal marsh literature have been established.

Several conclusions can be drawn from the research herein described:

1. Soil salinity increasingly constrains plant productivity when moving downstream from fresher parts of the Estuary to more saline areas. Overall plant productivity decreases with rising salinity, and vegetation communities change to include more salt-tolerant species at the expense of glycophytes.
2. The relative zone of influence of tidal channels decreases downstream within the Estuary due to rising salinity. This results in a compression of the streamside zone of vegetation and a channel-ward shift of transition zone communities as Estuary salinities rise.

3. Given adequate soil water availability, tidal marsh plant species within the Estuary are limited in productivity by relative soil salinity. Where soil salinity levels are lower, competition for light, particularly in the streamside zone, is an important productivity-limiting factor.
4. Primary productivity and subsequent additions to soil elevation through belowground biomass accumulation are important to the maintenance of tidal marsh elevations in areas away from the streamside zone. Deposition of imported sediments in higher marshes of the Estuary is largely restricted to the streamside zone.

Coincident with these conclusions are several caveats, which underscore the need for further investigation into the nature of tidal marsh geomorphology within the Estuary:

1. The influence of overmarsh floodwater versus groundwater movement on relative rooting zone pore water salinity is unknown. Relationships between tidal channel water elevation and rooting zone water table elevation are uncertain. It is suspected that groundwater movement plays a role in moderating salt stress in areas infrequently reached by overmarsh floods.
2. Larger-scale regional meteorological events, such as El Niños (ENSOs) were not encountered during the course of these investigations, and their effects are unclear. It is suspected that freshening of the Estuary occurs with increasing precipitation during El Niño events, potentially allowing expansion of less salt-tolerant species in otherwise salt-limited zones or areas.
3. The effect of reduced upland sediment supplies associated with upstream water diversion or increased water impoundment within the Estuary is unclear. Given that sediment deposition in the streamside zone is largely from exogenous sources, this zone is likely to show decreases in sediment accumulation with reduced stream sediment loads.
4. Homogenization of upper Estuary salinities through the adoption of water quality regulations was not directly investigated. Historically, Estuary

salinities fluctuated according to precipitation, runoff, and sea level influences, but have been more regulated recently through management of State and regional water resources. It is suspected that water management activities exert influence on soil salinities throughout the Estuary, and can thereby influence the nature and zonation of vegetation within associated tidal marsh ecosystems.

It is evident that continued management (or manipulation) of Estuary salinity has direct implication for tidal marsh maintenance and evolution. Soil pore water salinities exert proximate control over primary productivity in tidal marsh plant communities from the Sacramento/San Joaquin River Delta to the Golden Gate inlet in San Francisco Bay. The nature and character of tidal marsh ecosystems within the Ecoregion depend upon patterns of soil salinity within the Estuary – patterns that are currently under only partial managerial control.

Restoration efforts aimed at reestablishment of tidal marsh vegetation within the San Francisco Bay Estuary have only partially incorporated the concept of the interaction of biological and physical determinants of marsh ecosystems. Reestablishing ecosystems that respond to changing geomorphic and climatological conditions demands periodic revision of success criteria, from both the managerial and compliance viewpoint. Further, as found through the execution of the research described here, regional programs for restoration of local tidal marshes need to incorporate local ecosystem responses to regional physical gradients. Failure to do so will result in less than satisfactory restoration projects, locally as well as regionally.

Further recommended research to improve our understanding of local and regional variance of biological and physical interactions important to tidal marsh establishment and maintenance includes:

1. Investigation of the dependence of rooting zone hydrology on adjacent tidal channel hydrology, both in terms of water availability and in resulting soil pore water salinity.
2. Identification of the contribution of plant productivity to the accumulation of belowground biomass and maintenance of marsh plain soil surface elevations.

3. Identification of the physical and biological conditions under which invasion of tidal marsh ecosystems by invasive species occurs, and the degree to which these requirements are variable.

Incorporating this research into current and planned restoration programs should not be problematic, and will serve to further define our understanding of the importance of salinity on tidal marsh ecosystem function. Improving our understanding of the importance of hydrologic and salinity gradients in tidal marsh restoration efforts within the San Francisco Estuary can only serve to improve region-wide restoration success.